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ARISTOGENESIS, THE CREATIVE PRINCIPLE IN THE ORIGIN OF SPECIES[1]

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"Science is the asymptote of truth. It approaches unceasingly and never touches. Nevertheless it has every greatness. It has will, precision, enthusiasm, profound attention, penetration, shrewdness, strength, patience by concatenation, permanent watching for phenomena, the ardour of progress, and even flashes of bravery. . . . But Science is series. It proceeds by tests heaped one above the other, and the thick obscurity of which rises slowly to the level of truth."—*William Shakespeare, by Victor Hugo.*

As the title of his epoch-making work Darwin chose "The Origin of Species" (1859) because, as conceived by Linnæus (1735), the "species" was the ultimate unit of Creation in the animal and plant world. *Nullae speciae novae* was the battle cry of the conservatives of pre-Darwin days, but what Darwin devoted his life to was the *origin of adaptations, not of species.* Species are simply the by-products of adaptations.

Adaptation and the origin of fitness carries us back with a gigantic leap over time to Democritus (450 B. C.), the opponent of the intelligent creative design of Anaxagoras (500–428 B. C.) and the proponent of fixed natural laws in a purely mechanical system. Attributed by Aristotle[2] to Anaxagoras is the mechanical notion that the uses of the human hand in the various arts have, through inheritance, played an important part in human

[1] This is the eleventh contribution by the author on the Origin of Species and the principles of biomechanical evolution as demonstrated in palaeontology. See Bibliography.

[2] Osborn, 1929, p. 61.

intellectual progress, that man came into possession of hands because of his outstanding intelligence, for hands are tools allotted by nature to whosoever is able to make use of them. In truth mechanical adaptation was the oriflamme from Empedocles (495–435 B. C.), the father of the evolution idea, through Anaxagoras, Aeschylus, Aristotle and Plato. The Greeks led the way in forming what may be called the proto-Darwinian "chance hypothesis," the proto-Lamarckian "inheritance of acquired adaptations" hypothesis, and finally the "entelechistic" doctrine of natural law tending to perfection. The progressive improvement or retrogressive degeneration of human and animal mechanisms were the guideposts to the use and disuse inheritance speculations from the naturalists of Greece and Rome to Erasmus Darwin and Lamarck, the formulator of the "Lamarckian hypothesis."

Is it not astounding to find Aristotle (384–322 B. C.) debating proto-Darwinism versus proto-Lamarckism, just as Haldane and T. H. Morgan to-day are debating and upholding neo-Darwinism versus Kammerer and Mc-Dougall who are reviving neo-Lamarckism? Aristotle clearly defined proto-Darwinism in the sentence: "It is argued that where all things happened as if they were made for some purpose, being aptly united by chance, these were preserved, but such as were not aptly made, these were lost and still perish."[3] Aristotle also defined proto-Lamarckism: "Children resemble their parents not only in congenital characters, but in those acquired later in life. For cases are known where parents have been marked by scars, and children have shown traces of these scars at the same points. . . ."[4]

Liberally expressed, Aristotle's prevailing induction from his own observations was ". . . the idea of the development of the potentiality of perfection into actuality, the creation of form in matter. Nature does nothing

3 Osborn, 1929, p. 74.

4 *Idem*, p. 75.

without an aim. She is always striving after the most beautiful that is possible. . . . This perfection is the outcome of an all pervading movement.''[5] This movement we now term the ''internal perfecting tendency'' or ''entelechy.''

How tantalizing are these Greeks in anticipating every phase of modern speculation, amplified but not radically altered by our ''neo-Darwinians,'' ''neo-Lamarckians,'' ''mutationists'' and ''geneticists,'' ''entelechists'' and ''vitalists,'' all of whom feel the magnetism of the eternally baffling problem of the origins of adaptations. I too, for the past thirty-three years a hunter of fossil titanotheres, of fossil mastodons and elephants, concerned with the origin of the masterful horns of the titanotheres—of the superb tusks in the elephants, of the marvelous proboscis, of the supreme mechanical adaptations of the great grinders which grind uninterruptedly for over a century—love to feel that in part at least I have answered Aristotle's question:

''What, then, hinders but that the parts in Nature may also thus arise? For instance, that the teeth should arise from necessity, the front teeth sharp and adapted to divide the food, the grinders broad and adapted to breaking the food into pieces.''[6]

If any intellectual creed—for scientists have their creeds as well as theologians—may be slain by forty-three years of broad and intensive observation on the actual modes of the origin of species it is the Empedoclean creed of ''chance.'' Whatever may be true of the origin of the biophysical and biochemical adaptations of life, it is now positively demonstrated that Nature in her origin of species never gambles or takes a ''chance mechanical adaptation.''

The Biomechanist Replaces the Mechanist

The prefix *''bio''* is equally essential in animal mechanics, physics and chemistry; we are dealing with bio-

[5] Osborn, 1929, p. 79 (slightly modified).

[6] *Idem,* p. 74.

physical, biochemical and biomechanical phenomena ever acting, reacting and interacting; yet we have no inkling at present how these bodily movements affect the germ. Meanwhile is it not a significant fact that long prior to modern discoveries in biophysics and biochemistry of *liaison,* correlating, interacting and coordinating processes, naturalists like Hyatt, Cope and Osborn were applying mechanical and physical terminology to paleontological processes?

Bohr: In the recent language of the great physicist Bohr, organic mechanism is clearly distinguished from inorganic mechanism:

> On this view, the existence of life must be considered as an elementary fact that cannot be explained, but must be taken as a starting point in biology, in a similar way as the quantum of action, which appears as an irrational element from the point of view of classical mechanical physics, taken together with the existence of the elementary particles, forms the foundation of atomic physics.[7]

To borrow Bohr's metaphor life is a *"quantum"* of adaptive action, reaction and interaction. Before life appeared on our planet not a single combination of energy and matter was capable of resisting shock, of repairing waste, of combatting disintegration, of coordinating reaction or resistance. Organic mechanisms differ from inorganic mechanisms, no matter how perfect, in being more or less self-adapting, self-repairing, self-regenerating, self-modifying—also reaching into the higher powers of self-resourcefulness, self-experimenting, self-perfecting and self-creating! All these powers may be grouped under the single compound word auto-adaptation.

These auto-adaptational powers are exerted only in the living and cellular tissues which contain the hereditary geneplasm. Such tissues as the giant grinding teeth and tusks of elephants, which in the course of hardening lose their geneplasm, do not repair waste or show any power of regeneration, yet we shall demonstrate that such non-geneplasmic tissues may attain the highest degree of bio-

[7] Bohr, 1933, p. 458.

mechanical perfection and may evolve far more rapidly than any other part of the organism.

Planck: Modern mechanics affords us, says Planck,[8] the newest concepts of force, of acceleration, of retardation, or of inertia, and of mass: "The main object of mechanics is to find the motion which results from a prescribed cause."[9] The intensity of "force," for example, in producing a muscular change is causally related to the amount of acceleration, the cause of the "acceleration" being the " 'force' which we exert."[10] More intense muscular exertion corresponds to greater acceleration; a constant between force and acceleration is the inertia of mass; inertia or retardation are the opposites of acceleration; matter, momentum and energy are no longer three, but are fused into a single law, that of the conservation of energy.

Hopkins: Similarly, modern biochemistry is affording us a vista at least of the chemical bases of adaptive action, reaction and interaction in animal mechanisms. A synthesis of outstanding generalizations may be made from Hopkins' recent address on "Some Chemical Aspects of Life,"[11] as follows:

Life's advent is the most significant event in the history of the universe; life obeys the second law of thermodynamics, in its energy flow it provides *potential* activities; of equal importance is *organization;* among its various means of trapping and transforming radiant energy are chlorophyll, autotrophic and purple bacteria. Every living unit is a transformer of energy however acquired; the energy is tranferred from one reacting system to another; the energy of reactions is converted into mechanical responses. Ordered reactions are observed in cells and tissues rising from the stage of bacteria to the brain; surface colloids containing catalyzers control

[8] Allen, 1933, pp. 495–497.
[9] *Idem*, p. 496.
[10] *Idem*, p. 496.
[11] Hopkins, 1933.

reactions. Not equipped with catalysts, every living unit
would be static. Catalysts convert living systems into
transformers of energy and played an indispensable part
in the earliest stages of evolution. Molecules are ac-
tivated in entering some path of catalytic or enzymic
change. Kinetic evidence indicates that chemical
enzymes and related molecules precede *activation*. The
living cell is the seat of a multitude of highly organized
reactions; the selection or discrimination between mate-
rials is the specificity of cell catalysts; specific catalysts
not only promote reactions but also determine their di-
rection. The exact *coordination* within the living cell is
determined by the influence of special molecules as well
as enzymic or catalytic control; individual tissues, dif-
ferent in function, separate in space, so react upon one
another as to coordinate the activities of the body as a
whole; in coordination, beside the messages of nerves,
certain active substances carry chemical messages from
organ to organ, primarily hormones, each with properties
primarily chemical and physiological, *e.g.*, thyroxin,
adrenalin, secretin, insulin, hormones coordinating the
phenomena of sex; hormones coordinate the activities of
other hormones, produced within the body, while vitamins
come from the environmental diet. Certain species
synthesize their own vitamins, thereby becoming hor-
mones; converted by ultra-violet radiation, Vitamin D
controls in particular the growth of bone, (H. F. O.:
of interest therefore in the alloiometric growth of the
limb bones of elephants and horses.) Finally there are
the *organizers* of Spemann, rising from a group of cells
and inducing differentiation in other cells.

Linnæan Classification the Expression of Adaptation

The fossil vertebrates first afforded the most convinc-
ing proofs of the law of evolution as Darwin dreamed
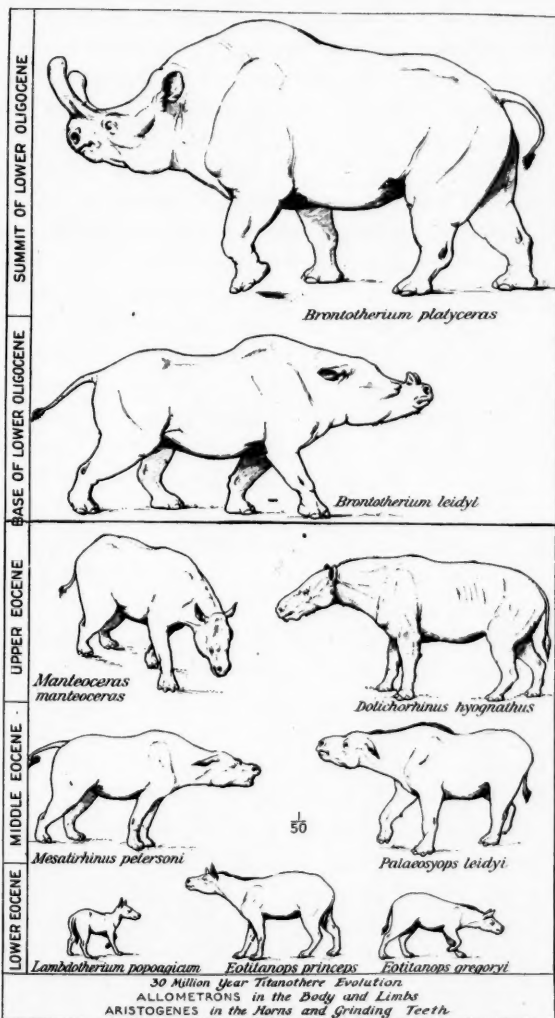and as Huxley in part witnessed. Centering around

FIG. 1.   ARISTOGENES AND ALLOIOMETRONS IN TITANOTHERES

Alloiometrons (new proportions of cranium and limbs) and Aristogenes (new horns and dental cusps) arise in the 30,000,000 year adaptive radiation of the Titanotheres, from the small Lower Eocene *Lambdotherium* to the gigantic Lower Oligocene *Brontotherium*.   All subfamily, generic and specific stages are defined by these two kinds of characters.   After Osborn 1929: 800, Chap. 1, Fig. 27.

adaptations in the vertebrate class, including fishes, amphibians, reptiles, birds and mammals, are the definitions of species, genera, families and orders. Through forty-three years of intensive research, especially on the evolution of the horse, rhinoceros, titanothere and elephant, we have now perfectly clear concepts of what the formerly dry systematic terms "species," "genera," etc., mean. Paleontology revivifies these terms with principles of potentiality, of acceleration, of the coordinated significance of every adaptive process. Neither Darwin nor Huxley lived to see the results of intensive methods of analysis and synthesis introduced by the brilliant mind of the Russian paleontologist Kovalevsky in the year 1873. Such analysis after exploration on a world-wide scale in the five continents has afforded materials for the discovery of new and unexpected principles of biomechanical evolution.

In the present Sedgwick Lecture we are attempting to summarize four new biomechanical principles which confirm and extend all the older principles.

Principle I of Adaptive Radiation: New and extremely significant are two principles revealed by the biomechanical researches of Osborn and Gregory[12] on the limbs of the fossil and living hoofed animals. (1) Starting forty-five million years ago with small, primitive, ambulatory, low-bodied mammals, which walk, shuffle or run clumsily, there diverged (2) mediportal quadrupeds with speed and pace of intermediate type tending to diverge in two directions; (3) graviportal quadrupeds, increasingly massive and gigantic, which swing the limbs ponderously in a walk or amble; (4) cursorial, swift, light-limbed quadrupeds which trot, gallop and leap and spring; and (5) aquatic mammals, low-bodied, short-limbed with weakened scapular and pelvic arches. From the dawning comparative anatomy of Aristotle to the specific definitions of Linnæus, these five locomotor types of quadrupeds

[12] Osborn, 1929: 800, Volume II, Chapter X.

have been recognized. Now for the first time, through very intensive alloiometric methods in the titanotheres, elephants and horses, *we know how these highly divergent locomotor types evolve biomechanically.*

The Mathematics of Limb Adaptation

For the first time in the 2,380 years of evolutionary speculation principles of phylogeny or animal descent become truly scientific when we can measure and number them in the sense of Francis Galton. The complete family evolution of the titanotheres reveals a fatally inadaptive grinding tooth structure, which after a period of a million years caused extinction. In widest contrast is the marvelous perfection and differentiation attained in the upper and lower ivory tusks of the mastodonts and elephants, accompanied by the most superb grinding teeth that nature has ever produced, yet after thirty million years both mastodonts and elephants finally suffered extinction from all parts of the earth, excepting only the single living species of Africa and of southern Eurasia. During the past thirty-three years an opportunity quite without precedent in the whole history of biology has enabled us to replace more or less wild and random evolutionary speculations, and hypotheses of the past, by observations, inductions, generalizations and principles of measurement of the rates of evolution soundly established in the titanotheres, verified, confirmed and extended in the proboscideans.

With the constant aid of William King Gregory we have applied both to the skulls and limbs the principle of measurement under the Greek term "alloiometry" signifying the measurement of the always differential changes of proportion, with most significant new results in the widely contrasted heads, limbs, feet and teeth of the titanotheres and of the proboscideans.

Alloiometrons may now be clearly defined, as follows:

Alloiometrons are not governed or predetermined by germinal potentiality in certain lines of racial, specific, generic, family and ordinal descent. On

the contrary, within species and even within races diverse alloiometrons or more or less profound changes of proportion, are independently arising. Alloiometrons are relatively rapid in development or temporal.   The term alloiometron (Greek ἄλλοιος "*of another sort or kind, different*" and μετρον "*to measure in any way*") signifies changes of proportion or intensity which may be expressed in measurements and indices, for example the proportional changes of the head expressed in the Greek terms brachycephaly (broad headed), dolichocephaly (long headed), brachyopy (short faced), dolichopy (long faced), bathycephaly (deep skulled), hypsicephaly (high skulled), etc., or in the limb proportions brachydactyly (broad fingered), dolichodactyly ·(long fingered), leptodactyly (slender fingered), dolichopody (long footed), brachiopody (short footed), dolichomely (long limbed), brachymely (short limbed), etc., or in tooth proportions brachyodonty (short toothed), hypsodonty (long toothed), etc.

The skull in mammalian species is primarily distinguished by diversely adaptive "alloiometrons"; experiment as well as specific analysis shows this.   The first changes in new races are *proportional* differences. In fossil lines of descent we observe this on a large scale. In the titanotheres the abbreviation of the face (brachyopy) and elongation of the cranium (dolichocrany) are in the widest contrast with the equine elongation of the face (dolichopy) and static condition of the cranium (brachycrany).   The heads both of titanotheres and of equines are in still wider contrast with the extreme shortening (brachycephaly), deepening (bathycephaly), heightening (hypsicephaly) of the elephant skull which affords a lever of the first order for the muscular force of the *longissimus dorsi* muscles which control the lifting, uprooting and other powerful actions of the ivory tusks.

The limbs of both the giant titanotheres and elephants are of the slow-moving, weight-carrying "graviportal" type in quadrupeds with massive limbs and short feet. The alloiometrons of the titanothere limb segments are not so very dissimilar to those of the elephants, but both titanotheres and elephants present the widest possible graviportal contrasts to the cursorial alloiometrons of the equines, deer and antelope.   *Equus* shares with all other swift-footed vertebrates the short thigh and arm bones and long lower limbs, while *Elephas* shares with all
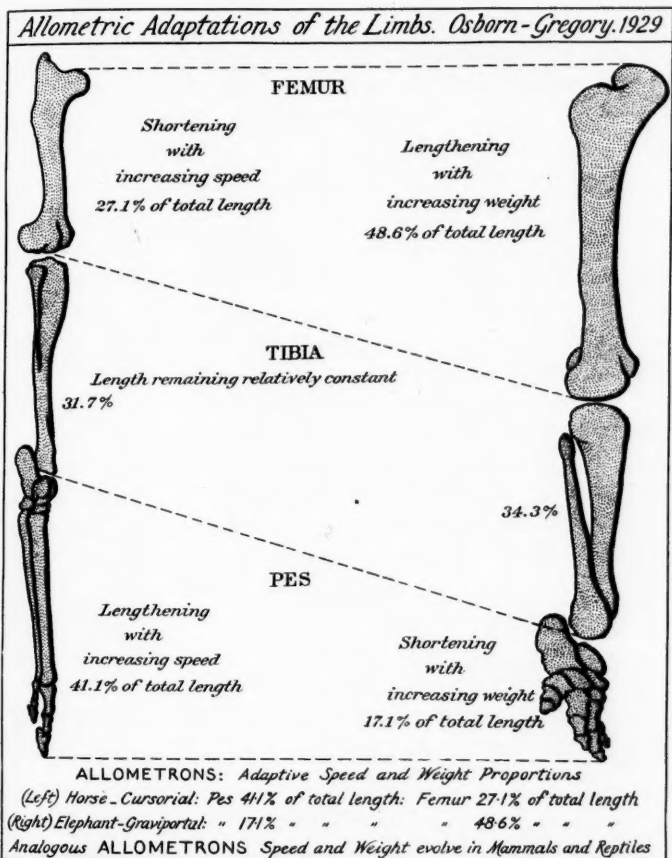
Allometric Adaptations of the Limbs. Osborn-Gregory.1929

FEMUR

Shortening
with
increasing speed
27.1% of total length

Lengthening
with
increasing weight
48.6% of total length

TIBIA
Length remaining relatively constant
31.7%

34.3%

PES

Lengthening
with
increasing speed
41.1% of total length

Shortening
with
increasing weight
17.1% of total length

ALLOMETRONS: *Adaptive Speed and Weight Proportions*
(Left) Horse - Cursorial: Pes 41.1% of total length: Femur 27.1% of total length
(Right) Elephant-Graviportal: " 17.1% " " " " 48.6% " " "
Analogous ALLOMETRONS *Speed and Weight evolve in Mammals and Reptiles*

Fig. 2.   Alloiometrons for Speed in the Cursorial Horse:
For Weight in the Graviportal Elephant

	Speed: *Equus*	Weight: *Elephas*
Femur	Shortened	Lengthened
Tibia	Constant	Constant
Pes	Lenthened	Shortened

In the proportional limb evolution of all quadrupeds, reptilian and
mammalian, we observe closely analogous changes of proportion. After
Osborn 1929: 800, Chap. IX, Fig. 670.

heavy slow-moving vertebrates the long thigh bone and the short lower limb. The elephantine alloiometrons (femur 48.6 per cent.; tibia 34.3 per cent.; pes 17.1 per cent.) are similar to those of the giant dinosaur *Camarasaurus* Osborn,[13] namely: femur 48.6 per cent.; tibia 33.7 per cent.; pes 17.7 per cent.

GRAVIPORTAL DINOSAURS AND ELEPHANTS. CLOSE PARALLELISM OF LIMB RATIOS

	Brontosaurus	Camarasaurus	Diplodocus	Elephas
Total length of hind limb, out-stretched	100	100	100	100
Length of femur	48.5	48.6	48.5	48.6
Length of tibia	32.0	33.7	35.2	34.3
Length of pes	19.5	17.7	16.3	17.0
Tibiofemoral ratio T/F	66	69	72	60
Metatarsofemoral ratio Mt. III/F	12	13	24	13
		Dinosaurs		Elephants

Close parallels with the equine alloiometrons are those of the swift-footed deer, antelope and gazelle.

Deus ex Machina; THE STATIC AND KINETIC ENGINEER

In a proverbially accepted sense the classic term (Latin) *machina* and (Greek) μηχανη signifies the tricks, artifices and stratagems[14] by which the gods rescue us. In the good sense, which we may here apply metaphorically in the evolution of limb proportions, *machina* signifies "means, expedient, device, contrivance,"[15] a machine effecting any particular purpose. In this good sense life is the *deus ex machina* in the solution of the innumerable biomechanical adaptations presented by the limbs of mammals in their progression through water, over the land and into the air.

[13] Osborn, 1921: 517.
[14] White, 1903, p. 360.
[15] *Idem,* p. 360.

Only for a moment can we dwell on the problems of adaptive reaction to tension, compression, shear, bending under transverse load, combined bending and twisting, straight lines for bones exposed to tension and compression, circular cross-sections for all parts in torsion, uniform fiber stress for parts subjected to bending (*e.g.,* the enamel fibers in the tusks of elephants).[16] In accordance with engineering requirements the thigh-bone of the titanothere and elephant resists compression, tension, torsion, bending in variable combination, hence its shaft is straight, its section circular, its hollow interior elliptical, its head anteriorly composed of arched fibers. The fore and hind limbs as a whole require a *frame* afforded by the arched ribs and the more or less cantilever structure of the backbone.[17] Thompson (1917) and Gregory (1933) observe in the backbone an analogy to the cantilever carried to the *nth* degree in the backbone of the big sauropod dinosaur *Diplodocus,* in which we find the T iron, the hollow cylinder, the stiffening ridges. In the mammal foot Thompson shows the stress lines. In the trabecular structure of the heel the bone is highly plastic, formed, deformed, demolished and formed anew; we do not agree with Thompson that "heredity" need not be invoked, for it is only in the tissues which retain the hereditary geneplasm that these reacting powers are displayed. In the skull the arch is the main architecture; in the horns, the logarithmic curved spirals. Only because of the necessity of the incessant nutrient supply through the blood vessels is the principle of the wheel and of the axle joint, controlled by elaborate check ligaments preventing complete wheel-like rotation, conspicuously absent in biomechanics.

As we pass from the static frame to the kinetics of the limbs, shown herewith in moving pictures from the Gobi Desert, ". . . the systems of compound levers and live springs comprising the locomotor apparatus are in equi-

[16] Paraphrase of Benjamin, 1908, p. 8, *et seq.*

[17] Paraphrase of Gregory letter, December 18, 1933.

librium and doubtless an equation could be worked out with gravity and mass on one side and moments of muscular force on the other. But when the antelope springs into the air it illustrates the principle of the catapult and the science of ballistics could supply the appropriate formula in which the weight of the animal, the height and the distance of the leap and the angle of elevation are known, while the foot pounds expended are to be determined. . . . A machine in action . . . must be provided with many kinds of movable joints, from sliding to hinge joints, and provision must be made for their constant renewal and lubrication. And since spasmodic action on one side of a joint would interfere with regulation and correlation of the machine as a whole, we find control effected by opposing flexors and extensors, etc.''[18]

The older testimony of comparative anatomy and embryology is enormously amplified by the testimony of paleontology, which is especially complete, over a period of five million years, on the ascending scale, in the speed ratios of the equines, *Eohippus* to *Equus*. The desert kiang, recorded by the American Museum expeditions in Central Asia, reaches a maximum speed of thirty-five miles an hour; a few individuals attain forty miles an hour for a short dash—perhaps a furlong; the limbs and body very much "collected"; with head held high and short quick strides; in a supreme effort lengthening stride and stretching out neck. Roy Chapman Andrews' films show a race with a fine stallion which several times reached forty miles an hour running side by side with the car. The speedy light-limbed bovines undergo analogous parallels and convergent alloiometric evolution with the equines, but, as shown in the Gobi Desert observations of Andrews, the higher speed ratios are attained in the timid desert gazelle rather than in the desert kiang. We know the exact length ratios of the upper, middle and lower limb segments which correspond to these speeds.

[18] Paraphrase of Gregory letter, December 18, 1933.

Cursorial Alloiometrons of the Hind Limbs in Equines and Gazelles

	Wild Ass	Gazelle
Femur	28.4 per cent. of total length	26.5 per cent. of total length
Tibia	28.2 " " " " "	30.9 " " " " "
Pes	43.4 " " " " "	42.6 " " " " "
	Maximum speed—35 to 40 miles per hour	Maximum speed—40 to 60 miles per hour

In comparison with the desert species of gazelle, the grassland species of the Gobi (*Gazella gutturosa*) is comparatively heavy-bodied, short-limbed; its maximum speed about forty-five miles an hour; the antelope shown in great herds are of the grassland species. The desert gazelle (*Gazella sub-gutturosa*) is a light-bodied, slender-legged animal reaching a maximum speed of about sixty miles an hour for a short dash—perhaps a furlong; it can maintain its normal running speed of about forty miles an hour. After three miles it settles down to a steady pace of about thirty-five miles an hour, which it can maintain for ten miles. Certain desert horses of America exhibit a tibio-femoral ratio of 117 which nearly attains the high-speed ratio of *Gazella dorcas*, namely, 125, or that of Andrews' Gobi Desert gazelle, namely, 133.

Principle II of Particulate Radiation: Every bone in every organ of every mammal adaptively reacts to its own particularly local and highly specialized mechanical problem; of two immediately contiguous bones, one may lengthen, the other may shorten; one may broaden, the other may become narrower. This separate, independent and particulate biomechanical response of each of the 280 bones composing the primitive ambulatory quadruped (*Phenacodus*) is precisely concordant with the particulate, separate, independent response of the four main enamel cones of the lower grinding teeth and of the six enamel cones of the upper grinders which furnish the aristogenic starting point of the marvelous biomechanical evolution of the proboscidean grinders.

These two principles of: (I) the independent adaptive radiation and of (II) the particulate adaptive response of each bony and dental element to its own mechanical problem renders wholly inadequate any theoretic application of diffuse *accelerating* (hormones) or *retarding* (chalones) chemical messengers. This inadequacy of any biochemical or biophysical interpretation at the present time is intensified when we take into account all the collective biomechanical principles discovered between the time of Aristotle and that of Von Baer, namely, the constant *coordination* and *correlation* with the biomechanical organism as a whole. To Aristotle we owe the two twin principles of *economy* and of *compensation* brought about through the *balance of progression* in the development of certain parts with the compensating *retrogression* in other parts. To Aristotle we owe the principle of *co-adaptation* and to Geoffroy St. Hilaire the hypothetic principle of auto-saltation or *discontinuity* under the sudden chemical changes in the environment. To Aristotle and Von Baer we owe the principles of acceleration and retardation in ontogeny; to Hyatt we owe these principles of acceleration and retardation in phylogeny. Goethe's poetic interpretation of the respective influence of heredity and of habit (auto-adaptation) on shape and form was applied to his discovery of the premaxillary bone in man:

> Thus by the animal's form is its manner of living determined;
> Likewise the manner of life affecteth every creature,
> Moulding its form.[19]

These multiple biomechanical principles, especially in respect to development and degeneration, were known both to Darwin and to Lamarck and were employed by them to illustrate their respective hypotheses as to the dominating influence of adaptive inheritance (Lamarck) and of adaptive selection (Darwin) in the origin of new species. Such principles were, however, exclusively ob-

[19] Osborn, 1929, p. 270.

served as somations or adaptations of the soma or body, *somatogenetic* or individual adaptations. It is now possible to observe them as *phylogenetic*, namely, during all the stages of their progression or retrogression over millions of years.

Entirely apart from adaptation through these incessant quantitative changes of proportion, of lengthening and shortening, of standardizing and improving, of progressing and retrogressing, of developing and degenerating, of selecting and eliminating, we are still shy of Darwin's main central problem as set forth above, namely:

THE ORIGIN OF NEW ADAPTIVE BIOMECHANISMS

Here we pass over the boundary of quantitative evolution expressed in alloiometrons into an entirely new and separate domain of research and generalization. In addition to the "secondary alloiometrons" just considered let us now observe the "primary aristogenes." The discovery of aristogenes was adumbrated before the now venerable Society of Naturalists forty-three years ago in the concluding sentence of Osborn's paper entitled, "Are Acquired Variations Inherited?": "Disprove Lamarck's principle and we must assume that there is some third factor in Evolution of which we are now ignorant."[20] This previously unknown factor proves to be aristogenesis; it was first known under the term "definite variation" (1890), then in 1908 as "rectigradation."

As briefly contrasted the definitions of alloiometrons and aristogenes are as follows:

Alloiometrons are new modifications in form and proportion of more or less ancient aristogenic characters. Alloiometrons are tetrakinetic in origin, that is, subject to the interaction of the four forces of (a) physical environment; (b) living environment; (c) influences of habit; (d) predispositions and potentialities of heredity.

[20] Osborn, 1897: 125.

Aristogenes are new adaptive units originating directly in the geneplasm and slowly evolving into important functional service. We know how these aristogenes arise, but we do not know why they arise, *i.e.,* their causes.

Aristogenes are governed or predetermined by germinal potentiality in certain lines of racial, specific, generic, family and ordinal descent. The term aristogenesis is derived from the Attic Greek ''aristos'' ($\alpha\rho\iota\sigma\tau\sigma$) signifying ''*best in its kind.*''[21] The Greek ''genesis'' ($\gamma\epsilon\nu\epsilon\sigma\iota\varsigma$) from the Aryan base meaning ''*to produce, bring into being*'' means ''*origin, source, birth, descent; . . . mode of formation or production.*''[22]

Aristogenesis is a creative process from the geneplasm of entirely new germinal biomechanisms; the process is continuous, gradual, direct, definite in the direction of future adaptation. In time contrast to alloiometrons which appear to be immediate and more or less temporal adaptive reactions to new habits, aristogenes are secular, appearing very slowly in the course of long periods of geologic time. Lines of ordinal, family, generic and specific descent may be distinguished by the potentiality of certain new geneplasmic aristogenes.

Aristogenic Titanothere Horns: Two of the principles controlling aristogenes were first demonstrated in the origin of the bony horns of titanotheres, namely, that while (a) potentiality, (b) predisposition and (c) predetermination control the definite origins of the horn rudiments, these rudiments do not appear simultaneously in diverse lines of phylogenetic descent but in intervals of time widely separated geologically, perhaps by thousands or hundred thousands of years. The ''emergence'' of these ''novelties,'' to paraphrase Lloyd Morgan's philosophic induction, is economically coordinated with the strength or weakness of the canine tusks; for example, in generic phyla of titanotheres where the tusks are sharp and powerful the horn rudiments are retarded in appearance and subsequently in development (gen. *Menodus*); conversely, where the tusks are blunt or feeble the horns are precocious and powerful (gen. *Symborodon*). This accords with Aristotle's twin principle of economy and compensation, which he expressed as follows:

[21] Liddell and Scott, 1883, p. 218.
[22] Wyld, 1932, pp. 476–477.

"Having now explained the purpose of horns, it remains to see the necessity of matter, by which Nature gave horns to animals. . . . We see that Nature taking away matter from the front teeth has added it to the horns."[23]

In the whole field of comparative anatomy and zoology no wider contrast could be afforded than the adaptive evolution and radiation of the titanotheres intensively studied in the Titanothere Monograph for the United States Geological Survey, and the adaptive evolution and radiation of the Proboscidea now in preparation for the Memoirs of the American Museum of Natural History.

It is this very contrast in the alloiometry of the skull, incisive tusks, the nasio-labial region, the aristogenesis of the grinding teeth, between the titanotheres and the proboscideans which throws a flood of light on the origin of adaptations and enables us to sharply distinguish between aristogenesis and alloiometrons.

The proboscideans rank next to man in biological importance and far surpass the mechanically inferior man in demonstration of all the main principles of biomechanical aristogenesis and alloiometry. It is difficult to circumscribe aristogenesis and alloiometry within their respective originating and modifying spheres of action, but there are certain lines of generic descent in which aristogenesis, for a long period of time, is the sole and dominating principle.

Revolutionary Progress in Phylogeny Since Darwin's Time

Darwin's species stood apart like isolated mountain peaks, whereas today living species and subspecies are often comparable to mountain chains, composed of lesser peaks completely connected by ridges known as "intergradations." It is not the number of species and subspecies which is significant, but the facts as to habit and habitat which are recorded with them. Similarly, it is not the number of fossil species now known as compared with those of Darwin's time, but the *linkage* of families, genera, species, subspecies, and even of "ascending" and "descending mutations" reaching back over hundreds of thousands, if not millions, of years.[24]

[23] Osborn, 1929, p. 72.

[24] *Idem*, 1926: 693, p. 337.

In the year 1827, shortly before Darwin began his voyage as a naturalist, Lesson recorded only 1,124 living and fossil species of mammals. In 1859, when Darwin's epoch-making work appeared, only one species of titanotheres had been described by Leidy, namely, *Titanotherium proutii* Leidy, 1852; the phylogeny of twenty-one genera and sixty-six species of titanotheres are described in Osborn's Titanothere Monograph.[25] Darwin in 1859 knew of only three genera of Proboscidea; *Deinotherium*, *Mastodon* and *Elephas*. These three genera included eleven species altogether, as shown in Fig. 3. In Os-
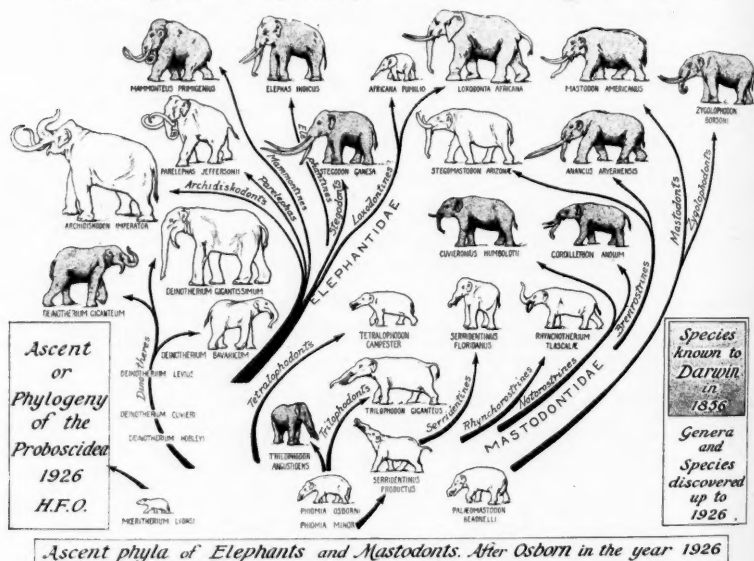
Ascent phyla of Elephants and Mastodonts. After Osborn in the year 1926

FIG 3.   PROBOSCIDEAN PHYLA OR LINES OF DESCENT: 1926

Shading: Species of *Elephas*, *Mastodon* and *Deinotherium* known to Darwin up to the year 1856.

Outlines: Genera and species known to Osborn up to the year 1926.

In Darwin's time all the Mastodontoids were embraced within the single Cuvierian genus *Mastodon*. Darwin's *Mastodon* included only seven species in 1859 when he wrote his "Origin of Species;" it now includes twenty-three valid genera and not less than one hundred and eighty-two species, a very large number of species remaining to be discovered.

25 Osborn, 1929: 800.

born's forthcoming Memoir there will be described approximately forty-five genera and three hundred species of proboscideans which are now interpreted phylogenetically, or in ascending phylogenetic order, as shown in Figs. 3 and 5.

Thus if the increase in living species of mammals is twenty-fold the increase in fossil species of titanotheres and proboscideans is one-hundred fold.

Of still more significance as regards Darwin's problem of the origin of adaptations is our knowledge of no less than forty-five generic lines of proboscidean ascent in which the coordinated play of aristogenic and alloiometric origins can be followed in closely continuous phylogenetic order. The breaks between the surviving terminal twigs of the giant branching trees of proboscidean ascent disappear and the first grand result is the replacement of all Batesonian hypotheses of "discontinuity" and of breaks between species. These time-honored difficulties melt away like a block of ice in the glowing sun of observation of the actual modes of the phylogenetic origin of adaptations.

The world-wide migration of the Proboscidea into all the continents except Australia, during the forty million year period from the upper Eocene dwellers on the ancestral Nile River and Lake Moeris in northern Africa, affords an unparalleled opportunity of studying the adaptive reactions to changing environmental influences. Climatically they vary from the south temperate and abundantly watered upper Eocene through the diminishing forests and moisture into the increasingly arid Pliocene and finally the severe climate of the Pleistocene. We now understand paleo-ecology almost as well as recent ecology. The reactional picture of the changing environment is less apparent in the body and in the limbs which become increasingly heavy and graviportal, but it is very obvious in the three organs of the head to which the entire body is subservient; the skull and jaws

Mastodontoidea: Adaptive Radiation from Genus Mastodon Cuvier, 1806. 23 generic phyla: Osborn, 1933
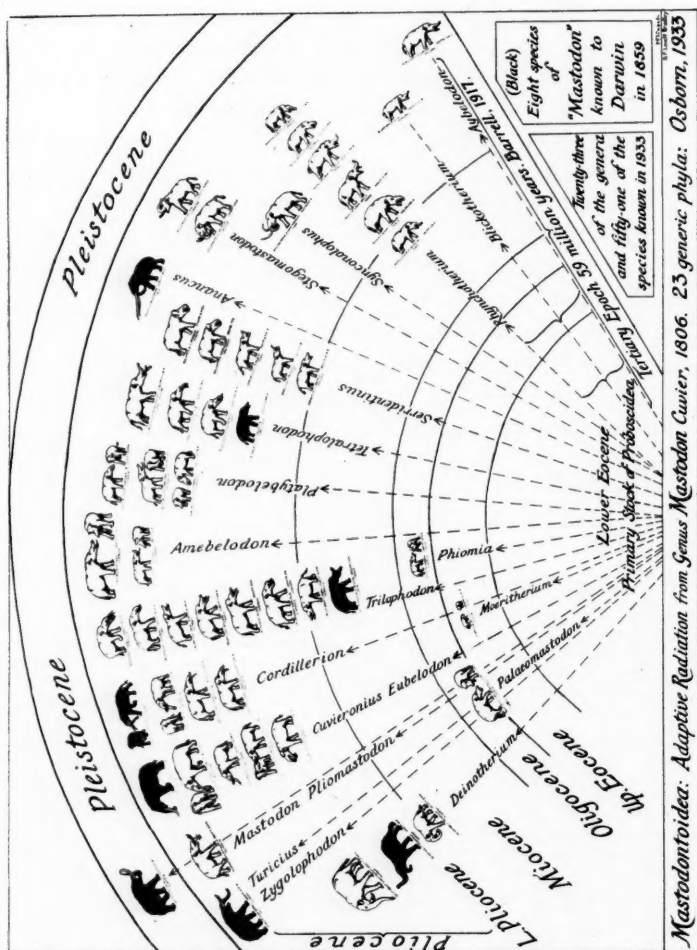
FIG. 4. MASTODONT PHYLA OR LINES OF DESCENT: OSBORN 1933

Black: Seven species of Mastodon known to Darwin up to the year 1856.

Outlines: Twenty-three genera and one hundred and eighty-two species known to Osborn in the year 1933.

Seventeen of these adaptively radiating lines of generic divergence from the ''Lower Eocene Primary Stock of Proboscidea'' were known to Osborn in April, 1933. In the succeeding Figure 5, twenty-three adaptively radiating lines of divergence are known in April, 1934, six having been discovered during the past year.

are also subservient to the coordinated functions and adaptations of (1) the tusks, (2) the naso-labial proboscis and (3) the grinding teeth. While the Proboscidea as a whole are under the broad principle I of adaptive radiation, the several organs evolve separately under principle II of particulate adaptive radiation. This is what actually happens in the forty-five separate lines of descent; we now know exactly *how* it happens, how adaptations and species originate; we do not know *why* it happens; before speculating as to the why and as to the nature of the inconceivably numerous chemico-physical modes of coordination let us glance at the three outstanding bio-mechanical centers, namely, the tusks, the proboscis and the grinding teeth.

Adaptive Radiation of the Tusks: Whereas the chief biomechanical problems of the titanotheres as analyzed by Osborn and Gregory center around the bony horns, the elephants and mastodonts are without horns but are provided with upper and lower tusks which, beside acting as weapons of offense and defense, adaptively radiate into an infinite variety of form and function in relation to the capture of food.

It is a universal distinction of Proboscidea that out of the primitive twelve incisor teeth, six upper and six lower, only the *second pair* above and below function and survive. In the aquatic Moeritheres of the Oligocene Lake Moeris of northern Egypt, which resemble the hippopotami in habit, these upper and lower tusks are of equal size and of similar function. But, under the prinple II of particulate adaptive radiation, in all other proboscideans the superior and inferior pair of incisors perform entirely diverse functions; these functions are of *eight* different kinds (1) In the beak-jawed mastodonts or Rhynchotheres of Africa, India and America, the long and enameled inferior incisors are upcurved and doubtless served an up-rooting function while the superior incisors became sharp offensive and defensive tusks. (2)

In the Deinotheres, which were not improbably fluviatile
or river-border in habitat, the superior incisors entirely
disappear while the gigantic inferior pair are down- and
back-turned like those of the walrus.   (3) In all the mas-
todonts related to the classic *Mastodon angustidens* of
Cuvier and the *Mastodon longirostris* of Kaup, as well as
in the newly discovered Serridentines, the superior in-
cisors are sharp, down- and out-turned tusks extremely
formidable as weapons, the dentine or ivory being
strengthened with a lateral enamel band.   (4) In the
mountain loving *Mastodon andium* group known to Hum-
boldt, Cuvier, and Darwin, the superior incisors form
long spirally-twisted tusks in which the enamel band fol-
lows the curved line of torsion.   (5) In all other mas-
todonts the superior tusks lose their enamel and become
rounded and up-curved like those of the American species,
named *Mastodon* by Cuvier and well known to Darwin;
these tusks are analogous to those of the *Mastodon hum-
boldtii* group of the Argentine and more or less to those
of the *Anancus brevirostris* group of Eurasia.   (6) The
lower incisors atrophy or entirely disappear in three
short-jawed groups of the mastodonts and in all the dif-
ferent short-jawed forms of elephants the double func-
tion of offence and defense and of the capture of food is
entirely assumed by the superior tusks.   (7) In four
groups of mastodonts the lower incisors take on a great
variety of functions such as (a) the uprooting of plants
in the Rhynchotheres; and (b) the prodding at the roots
of plants in the long-jawed Trilophodonts, known as
"prod-tuskers."   (8) Most extraordinary, however, is the
shoveling function which evolved independently in four
entirely distinct lines of descent.   The outstanding ex-
amples are (a) the Amebelodonts or "shovel-tuskers" of
North America, directly descended from the primitive
shovel-tusker *Phiomia* described by Andrews from the
Oligocene Lake Moeris of Egypt, (b) the Platybelodonts
or "flat-tuskers" independently discovered by Borissiak,
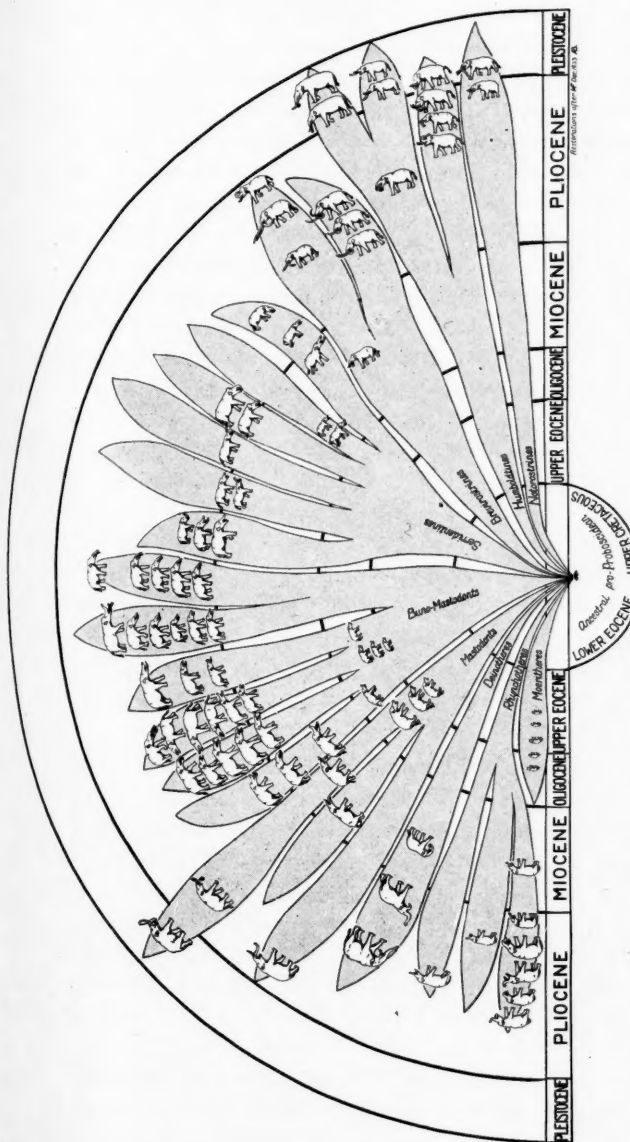
FIG. 5. MASTODONT PHYLA OR LINES OF DESCENT: OSBORN 1934

In this chart observe small black figure representing ancestral pro-Proboscidean of Lower Eocene or Upper Cretaceous time. From this diverged the Moeritheres (MOERITHERIOIDEA) of North Africa, the Deinotheres (DEINOTHERIODEA) of Africa and Eurasia, also seven great subfamilies of MASTODONTOIDEA originating in Africa and passing through Eurasia into North and South America, namely: Rhynchotheres, Mastodonts, Bunomastodonts, Serridentines, Brevirostrines, Humboldtines and Notorostrines, each distinguished by the surface pattern of the grinding teeth as well as by the divergent adaptations of the superior and inferior incisive tusks.

Granger and R. C. Andrews in the Desert of the Gobi. The three known species of *Platybelodon* exhibit a perfected pair of broadened chisels reinforced within by dentinal tubules, kept sharp by polishing the lower surface on smooth rocks; this pair of lower incisors combines to form a shovel twelve inches broad, in form exactly like a coal shovel.

Adaptive Radiation of the Proboscis: It has been assumed by all zoologists that all proboscideans evolved a proboscis and that ancestral proboscideans would show step by step the evolution of this remarkable organ. Accordingly in all current literature and popular restorations the proboscis is shown in its variable stages; in our restorations several entirely distinct modes of naso-labial adaptation are displayed. After the most intensive research it appears that there were three widely distinct naso-labial adaptations, namely, (a) the broad hippopotamoid upper and lower lips of the Eocene Moeritheres of Lake Moeris; (b) the flat extended upper lip of the flat-tuskers (*Platybelodon*) and of the shovel-tuskers (*Amebelodon*); (c) the typical rounded elephantine proboscis progressively extended until it reaches the ground and is capable of a great variety of functions.

The Moeritheres (a) were exclusively aquatic and did not need a proboscis. Contemporary with them along the borders of the Oligocene Lake Moeris of northern Egypt was the primordial "shovel-tusker" (*Phiomia*) in which the abrasion of the broadened upper lip (b) is clearly apparent on the upper surface of the flattened tusks; this labial abrasion of the lower tusks is also clearly apparent in the descendants of *Phiomia,* namely the flat-tusker of the Gobi Desert and the shovel-tusker of Nebraska (c).

It is probable that all other proboscideans, including the twenty-three different kinds of mastodonts, which up to recent time were all treated as belonging to the genus

Mastodon, evolved a more or less typical proboscis; it is also certain that all the elephantoids evolved a proboscis through parallel evolution. The elephantine proboscis arose in connection chiefly with the browsing habit and was retained even during the grazing habit of the woolly mammoth. Owing to the general likeness of the rounded superior tusks in many of the subfamilies of the mastodonts to those of the eight genera of the elephants, we turn to the adaptive radiation of the grinding teeth as the most distinctive means of distinguishing the genera and subfamilies both of mastodonts and of elephants. Figs. 4, 5 and 6.

Principle III of Adaptive Radiation of the Grinders: In the restorations of the twenty-three kinds (Fig. 5) of mastodonts it is the adaptations of the superior and inferior tusks combined with the·manifold adaptations of the grinding teeth which give us two outstanding results: first, from the biomechanical standpoint, tusk and grinder adaptations absolutely confirm the principle (II) of particulate adaptive radiation; second, these adaptations of the grinders and of the tusks combined afford a reliable means of determining both the habitat and the nature of the food supply which underlies the principle (I) of adaptive radiation of these animals as a whole.

Geneplasmic Potentiality: Still more characteristic of aristogenesis in the grinders is the kinetic principle of potentiality demonstrated in the ancestral geneplasm. All proboscideans in Eocene time start with four conical "aristogenes" typified in the lower molars of *Moeritherium* (Fig. 8); this to all appearance is like the equines starting with the four-coned molar of the ancestral horse *Hyracotherium* of the lower Eocene London clay. But differentiating this visible or phenotypic similarity is the widely divergent aristogenic *potentiality* of the primitive proboscidean and primitive equine molar; the adaptive fate of the four coned *Mastodon* molar is as far apart as

possible from the adaptive fate of the four-coned *Hyracotherium* molar, the one ends in the marvelously complicated 27 plated molar of the woolly mammoth, the other is fated to evolve into the double-columned grinder of the horse. When the lush Eocene and Miocene vegetation is supplanted by the drier Pliocene vegetation, both mammoth and horse resort to the same expedient of ptychoid infoldings of enamel, dentine and cement, to afford an always irregular grinding surface. This biomechanical device is a sample of convergence.

Mastodont Ridge Crests: The next problem is to convert the transversely placed cones into ridge-crests or lophs. In the thirty-eight known lines of potentially similar generic and subfamily proboscidean descent the same almost exclusively proboscidean mechanical device of binary division of each of the four cones into 2–4–8–16 conelets is repeated over and over again. But, following the principle (II) of "particulate adaptive radiation," in no genus or subfamily do the primary four aristogenes of the molar crown evolve into an exactly similar union, acceleration, retardation, folding or plication of the crests. Some primary cones and secondary conelets drop out of the ridge crests; other cones and conelets begin to show "trefoil" enamel foldings, such as were recognized by Cuvier as distinguishing Humboldt's Argentine mastodont (*M. humboldtii*) from the Andean mastodont (*M. andium*). While the plications in *M. andium* are limited and simple, those in the Argentine *M. humboldtii* finally cover the crown; in the related *M. mirificus* of Nebraska the foldings become ptychoid or labyrinthine. These biomechanical adaptations of unequally dense enamel-dentine-cement, to the comminution and grinding of herbage of different degrees of hardness, were sought in the adaptive radiation of browsing types of the forests and mountains (*M. andium*), in the grazing types of the Argentine plains (*M. humboldtii*) and in the arid herbage of the American plateaus (*M. mirificus*). Thus was

brought about the *ébranchement* of Lamarck, the *divergence* of Darwin and the *adaptive radiation* of Osborn. The twenty-three distinct generic phyla, into which Cuvier's single genus *Mastodon* has radiated, are displayed in Fig. 5 and each exhibits a grinding tooth crown sculptured as distinctively as the "cartouche" of the Egyptian monarchs. The second device to prolong life and prolong its gustatory joys is the vertical elevation of the crown known as *hypsodontism;* this appears to be an alloiometric or proportional process because it occurs independently in the grinders of many divisions of the hoofed animals.

During the progressive Eocene to Pliocene desiccation these ingenious dental biomechanisms of all the twenty-three genera of Moeritheres, Deinotheres and Mastodonts signally failed. In the northern hemisphere all adaptations failed, excepting three. ·Falconer's *Anancus* of East Anglia and Barbour's *Tetralophodon* of Nebraska alone survived into the lower Pleistocene. Our classic mastodont *M. americanus* alone survived into the dense humid forests of middle and eastern North America.

ELEPHANT RIDGE CRESTS

In the elephantoid division the low transverse ridge crest is perfected in the upper Pliocene of the African ancestral elephants (*Archidiskodon*). The unique aristogenic potentiality of the transverse ridge-crests to convert pairs of cones by transverse binary fision into transverse ridges is followed by the elevation of these ridge-crests into the elephantine ridge-plates, as first manifested in the roof-toothed *Stegodon* of southern Eurasia. It is paralleled in the distinct *Archidiskodon* ridge-plated stock of the upper Pliocene of South Africa. This dark continent gave rise to the world dominant elephantoid division of the Proboscidea. Until recently the elephantoids were grouped in only two genera—*Elephas* of Asia and *Loxodonta* of Africa but they are now known
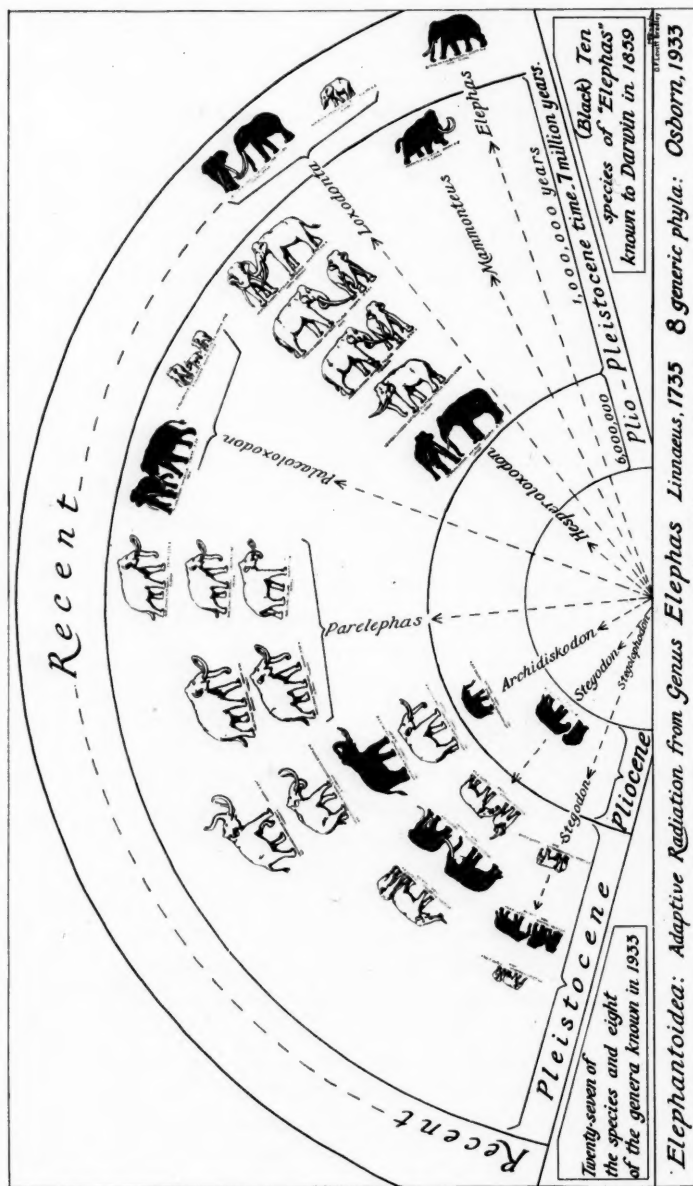
FIG. 6. ELEPHANT PHYLA OR LINES OF DESCENT: OSBORN 1933

Black: Ten species of the single genus *Elephas* known to Darwin in the year 1859.

Outlines: Radiating lines of descent of the eight genera of ELEPHANTOIDEA described in Osborn's memoir of 1934. In Darwin's time all the living and fossil Elephantoids were embraced within the Linnean genus *Elephas*. Darwin knew of ten species only, including Falconer's *Elephas ganesa* (now *Stegodon*). We have now determined (1934) not less than ten well-founded genera of Elephantoids and ninety-seven (plus 14?) species, a very large number still remaining to be discovered.

Elephantoidea: Adaptive Radiation from Genus Elephas Linnaeus, 1735   8 generic phyla: Osborn, 1933

to subdivide into six other genera, including the mammoths (*Mammonteus*) of the north, of the mid-temperate region (*Parelephas*), of the sub-tropical region (*Archidiskodon*) in which the elephantoid biomechanisms reach their climax; while the two remaining loxodontine genera, *Palæoloxodon* of the Orient and *Hesperoloxodon* of western Europe, are more conservative. Aristogenesis combined with alloiometric extension is carried to the biomechanical extreme in the divergently adaptive grinders of the three mammoths. The contrasts in the total length of the enamel foldings of the gigantic *Archidiskodon* (8,000 mm), of the gigantic *Parelephas* (10,000 mm), of the relatively small *Mammonteus* (6,000 mm) are coordinated with the relative intensities of their struggle for existence.
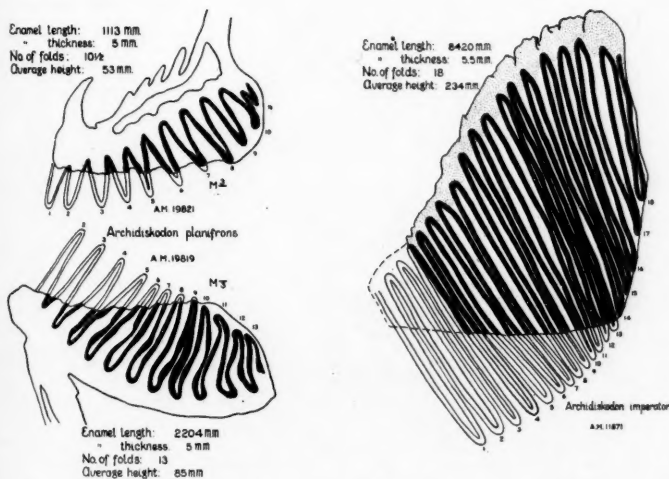
Fig. 7. Accelerated Elephantine Ridge Crests in *Archidiskodon*
Intensely accelerated evolution of the ridge plates from the *Archidiskodon planifrons* of southern Eurasia into the *Archidiskodon imperator* of the United States and Mexico, all occurring from Upper Pliocene to Middle Pleistocene time.   Length of enamel foldings:

Archidiskodon imperator of Texas = 8420 mm.
Archidiskodon planifrons of India = 2204
Archidiskodon planifrons of India = 1113

In these southern mammoths of Africa, Eurasia and North America, gigantic size is attained in a relatively short period of geologic time.

Reciprocal Biomechanisms: From the architectural standpoint the reciprocal grinding adaptations of the upper and lower grinding teeth in the mastodontoid as well as elephantoid Proboscidea affords the most striking example thus far discovered of *reversed structural resistance* to stresses and strains; every engineering detail of the upper grinders is reversed in the engineering de-
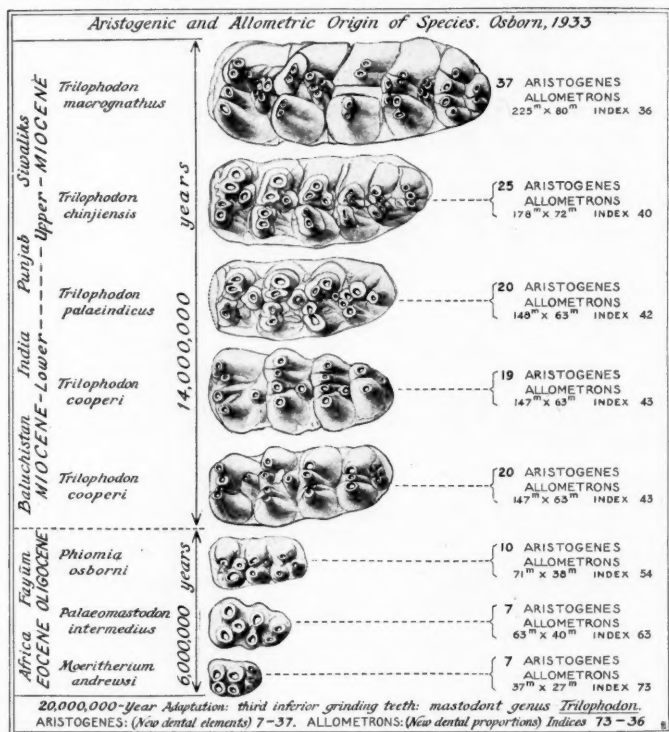
FIG. 8. ARISTOGENES AND ALLOIOMETRONS SLOWLY EVOLVING IN *Mastodon*

This retarded 20,000,000 year origin of Aristogenes in the generic phylum *Trilophodon* is in widest possible contrast to the accelerated evolution of the elephantine grinders of *Archidiskodon* shown in Figure 7; one Aristogene or new conical element appears in course of a million years. At the same time this unique fourteen million years generic phylum affords the most convincing proof of the creative principle of Aristogenesis which has thus far been discovered. Especially significant are the little cones arising in the valleys between the ridge crests as clearly shown in *Phiomia osborni* (10 aristogenes), *Trilophodon cooperi* (20 aristogenes), *Trilophodon chinjiensis* (25 aristogenes).

tails of the lower grinders; for example, an upper pre-
convex arch encounters a lower post-convex arch. The
Aristotelian principles of mechanical economy and com-
pensation are manifested in the most extraordinary man-
ner in the coordination of the adaptive radiation of the
tusks with that of the grinding teeth. Not an ounce of
mass, not a unit of energy is wasted, nor is there a single
ounce of surplus. In the shovel-tuskers the concentration
of force upon the great chisel-shaped incisors is com-
pensated for by the diminution of force in the grinders
and the entire upper part of the cranium.

New Aristogenes Added to Inferior Grinders in the Period Estimated at 20,000,000 Years

In a definitely known period of geologic time a
unique and outstanding example of aristogenic origin
from the geneplasm is witnessed in the Siwalik Hills
of northern India during the flood plain deposition
of 13,000 feet of Miocene sediment (Chinji 2,300 feet;
Kamlial 1,700 feet; Murree 8,000 feet; Gaj (Bugti) 1,000
feet); the percentage of these Miocene strata to the whole
Siwalik series of 16,000 feet is eighty-one; the time esti-
mate of the whole Miocene period (Barrell, 1916) is from
12,000,000 to 14,000,000 years; accordingly this aristo-
genic progress continued for 20,000,000 years altogether
(Fig. 8). We witness here the aristogenic origin from
the gene-plasm in a definitely known period of geologic
time, Oligocene to Miocene, of 24 new biomechanical units
which may be tabulated as follows:

		Ridge crests	Cones	Conelets	Conules	Trefoils	Total conical elements	Total new elements
Upper Miocene	*Trilophodon macrognathus*	5½	12	19	4	8	26	34
Middle Miocene	*Trilophodon chinjiensis*	5½	12	21	4	14	27	35
Lower Miocene	*Trilophodon palæindicus*	4⅕	10	17	3	6–7	20	27
Basal Miocene	*Trilophodon cooperi*	4⅕	10	17	2	0	19	19
Lower Oligocene	*Phiomia osborni*	3⅓	8	10	2	0	10	10

Principle IV of Adaptive Secular Reaction: The principle IV of adaptive secular reaction has very important theoretical bearings as we are pointing out in a summary of these observations.

Each of the aristogenes rises from the creative potentiality of the geneplasm, first as an inconspicuous rudiment, finally as a functional and useful cone or enamel folding. In the lower Oligocene *Phiomia osborni* the third inferior grinders, with the corresponding grinders above, condition the daily needs of crushing the requisite amount of herbage and are prophetic of the fact that in all proboscideans it is the back molars on which biomechanical adaptation concentrates. Nine new primary cones and secondary foldings are added in the Basal Miocene *Trilophodon cooperi;* seventeen aristogenes appear in *Trilophodon palæindicus;* twenty-five appear in *Trilophodon chinjiensis;* twenty-four in *Trilophodon macrognathus.* This phyletic series accordingly is a true picture of the evolution of the aristogenesis latent in the ancestral Oligocene geneplasm. The three principles of potential homogeny, of secular adaptive reaction, of the aristogenic creation of something more adaptive, are again demonstrated in the third inferior molars of a single line of descent.

The heredity principle of great significance in biomechanical evolution is that these new aristogenic primary cones arise only in the genera which are more or less closely affiliated by descent to the ancestral *Phiomia* of the upper Oligocene of Egypt; it is in this great family of Bunomastodonts that these particular conical aristogenes arise.

In all other divisions of the Mastodontoidea excepting the Bunomastodonts (Fig. 5) these particular aristogenes do not appear at all; the grinders adapt themselves in other ways to the biomechanical problems thrust upon them, either by evolving more or less sharp transverse crests as in *Mastodon,* in desert loving species of *Serridentinus* or

in *Turicius,* all of which genera feed by a chopping vertical motion of the jaws. Those which feed by a circular grinding motion of the jaws, *e.g., Anancus* and *Synconolophus* do not add aristogenes but increase the complications of the enamel surface by infoldings and plications.

The comparison of the origin of the conic aristogenes of the grinders of the proboscideans with the rudiments of the horns in the titanotheres demonstrates that the potentiality of raising an aristogene from its geneplasmic or genotypic stage into a visible somaplasmic stage is a matter of acceleration in contrast to the retardation which holds the potential aristogene within the geneplasm. Just as the horn rudiments in the titanotheres are observed to emerge at widely different intervals of geologic time, so the aristogenic cones in the grinding teeth of the proboscideans may appear very early as in the case of the Oligocene shovel-tusker *Phiomia,* or very gradually in the species related to the classic *M. angustidens* of Cuvier. In brief, each conic aristogene is a matter of particulate adaptive radiation.

Summary: What evokes an aristogene from the geneplasm is as mysterious to us as what evokes a horn rudiment in the skull of the titanothere. We remain in the present part of this address purely on observational and inductive grounds and simply make statements of fact or of principle without offering any explanation. Aristogenes certainly do not appear spontaneously or without any previous exciting or awaking cause. All that we observe is that the aristogenes are in sequence to new or changing environmental conditions of food. It seems to be a secular adaptive reaction, just as the appearance of the horn in the titanotheres is in secular adaptive reaction to the living biotic environmental conditions and the struggle with other animals.

Natural Selection not a Cause: The rapidity of evolution of the aristogenic elements in the grinding teeth is

now known to be independent of the intensity of selection
or elimination.   During the relatively brief Plio-Pleisto-
cene million and a half year period all the elephants were
protected by the superb development of their incisive
tusks; these tusks, together with the greatly superior
mechanism of the grinding teeth, enabled the elephants to
completely supersede or drive out the mastodont stocks
and to replace the mastodonts in all parts of the world
except South America and Australia from which they
were barred by impassable oceanic barriers.   In South
America only a single species (*Parelephas cayennensis*)
penetrated as far as French Guiana.   It is also known
that no species of elephant occupied the same geographic
range as another species at any given period of geologic
time; thus there was no competition between species.   So
far as we can judge the elephants were the most domi-
nant, resourceful, well-defended quadrupeds known at
any time in the earth's history.   The independence of
Selection as an originating cause in aristogenic evolution
is shown by the amazing rapidity with which the elephan-
tine grinding teeth evolved, this evolution far outstripping
that of the grinders of any of the contemporaneous rapidly
breeding animals.   Whereas it is often very difficult to dis-
tinguish a swift-breeding Lower Pleistocene rodent from
a modern rodent, the gap between the grinding teeth of the
slow-breeding elephants in the same period of time is
enormous.

Philosophical Inductions

It appears that aristogenesis is a matter of potentiality,
rather than of predetermination which is the essential ele-
ment in every entelechistic hypothesis.

Potentiality versus Predetermination: A recent def-
inition of the term potential is as follows: "Latent, un-
developed, but capable of developing and becoming effec-
tive; existing in the germ. . . ."[26]   While a purely

[26] Wyld, 1932, p. 894.

physical term, the mechanical term "potential" appears
to apply to the latency of the aristogenes both in the
grinding teeth of the Proboscidea and in the horns of the
titanotheres.   The presence of this latent power in the
germ or *genedynamy* is attested by the entire history of
the grinding teeth of the mammals extending back to the
single coned pro-mammals of the Triassic time.   In ob-
serving the aristogenic origin of cone after cone which
appears to culminate in lower Eocene time in a gener-
alized crown from which all the teeth of the hoofed mam-

FIG. 9.   ANCESTRAL MASTODONTS AND MOERITHERES OF THE PRIMITIVE
NILE RIVER

Compare Figure 5 illustrating divergence of each of these primitive Pro-
boscideans from a remote ancestral stock, the Moeritheres, small aquatic
Proboscideans, leaving no descendants.

Phiomia osborni (right), primitive shovel-tuskers, ancestral to the shovel-
tuskers *Amebelodon* of Nebraska.   *Palaeomastodon* (upper left), primitive
Mastodonts, ancestral to the true Mastodonts of Eurasia and North Amer-
ica.

mals descended, we uniformly derive the impression of
something which in time *may* appear.

It is interesting to note, on purely philosophical
grounds, that Aristotle, both in his own writings and as

interpreted by Augustine, looked only for the laws of nature, which were designated in his philosophy as "necessity." Augustine, as an evolutionist and disciple of Aristotle, rightly compared the work of creation with the growth of a tree from its seed, all parts springing up gradually. All things, he concluded, are in the seed, not by material substance but by *causal energy and potency,* including also "those things which the water and the earth produced *potentialiter atque causaliter.* . . ."[27]

Continuity versus Discontinuity: An interesting coincidence in the history of evolutionary causation is that while William Bateson was working in Cambridge after his graduation (1882) from St. John's, reacting from Weldon's tutelage, he independently turned to the study of variation chiefly on the materials afforded in the Cambridge museums, and in the introductory pages to his well-known volume gave his preliminary conclusions as follows:

This book is offered as a contribution to the study of the problem of Species. . . . The work was, as I have said, begun in the earnest hope that some may be led thereby to follow the serious study of Variation, and so make sure a base for the attack on the problems of Evolution. . . . If the Study of Variation can serve no other end it may make us remember that we are still at the beginning, that the complexity of the problem of Specific Difference is hardly less now than it was when Darwin first shewed that Natural History is a problem and no vain riddle. . . . These two facts constitute the problem: I. *The forms of living things are various and, on the whole, are Discontinuous or Specific. II. The Specific forms, on the whole, fit the places they have to live in.* How have these Discontinuous forms been brought into existence, and how is it they are thus adapted? This is the question the naturalist is to answer. To answer it completely he must find (1) *The modes* and (2) *The causes* by which these things have come to pass.[28]

At the same time Osborn, studying in Cambridge (1879–1880) and Princeton (1881–1890) was also interested in the problem of variation, and in opening a discussion[29] upon the Lamarckian principle before the

[27] *Cf.* Osborn, 1929, pp. 109–110, 111–112.

[28] Bateson, 1894, pp. i, xi, xii, 3.

[29] Osborn, "Are Acquired Variations Inherited?", 1891: 53.

American Society of Naturalists reached conclusions as to the existence of *definite lines of blastogenic variation,* as follows:

The conclusions we reach in this discussion must finally turn upon the existence of definite lines of blastogenic variation. If there are no such lines, the Lamarckian principle falls *ipso-facto*—if there are, we have still to estimate the probabilities between Weismann's and Lamarck's principles as affording the most adequate explanation for them, keeping in mind the problem of Inheritance [*i.e.* Heredity] as affecting these probabilities. The Weismann principle depends upon Selection as the source of definite lines of Variation. What evidence is there for the initial but all essential assumption, that, for example, a tiny adaptive cusp is a factor in survival, while its tiny inadaptive fellow is a factor in extinction? Not to mention the succeeding assumptions which overwhelm us *when we seek to derive definite adaptations from indefinite variations.* The Lamarckian principle furnishes us with an explanation of the observed phenomena of simultaneous progressive adaptation in most of those parts which it affects, including Correlation and Parallelism. It cannot be said at present to explain *all* the phenomena within its sphere; we must explain these phenomena, or abandon the principle. It follows as an unprejudiced conclusion from our present evidence that upon Weismann's principle we can explain Inheritance but not Evolution, while with Lamarck's principle and Darwin's Selection principle we can explain Evolution, but not, at present Inheritance. Disprove Lamarck's principle and we must assume that *there is some third factor in Evolution* of which we are now ignorant.[30]

Thus Osborn and Bateson laid out for themselves a program for future research, based in Bateson's case on *the concept of discontinuity between species,* and in Osborn's case on the concept of the existence of definite lines of blastogenic variation still to be discovered. Bateson rejected the adequacy of Darwin's principle of Selection, and Osborn, after a brief (1889–1895) pro-Lamarckian phase of speculation, soon reached the program of his present line of research as set forth in his Woods Hole address entitled, "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution."[31]

This research now attains a new starting point for future study in the principles set forth in the present Sedgwick Lecture.

[30] Osborn, 1891: 53, p. 20.
[31] *Idem,* 1895: 97.

The Biology of 1890 and of 1933

Addresses of this kind naturally take stock of the biological knowledge of the period. When we compare our biology of 1933 with our biology of 1890,[32] we have reason to feel very much encouraged. It is true that like Byrd and Ellsworth our voyage into the unknown is blocked by obstacles which can only be penetrated with great difficulty, but we are led forward by the human scientific instinct in the intellectual struggle for existence against the unknown, so beautifully expressed by Victor Hugo in the lines opening this address.

Our first source of encouragement is that we have put out of action several of the hypotheses of the 1890 period. We have proved that acquired variations are not inherited and that Lamarckism, if it survives at all, can only be in the form presented in the ''organic selection'' hypothesis independently arrived at by Lloyd Morgan, Baldwin and Osborn, namely, that somatic adaptability to modification in progressive directions is in itself a geneplasmic principle which, combined with the incessant action of selection, may lead into new and adaptive biomechanical organs. Another possible survival or variant of Lamarckism is the ''secular adaptive reaction'' to new conditions of habit and environment which we have spoken of in this address. Again, the extreme Weismannism of the 1890 period which placed the geneplasm in an environmental-proof enclosure has been replaced by the most positive evidence coming from field zoologists that the geneplasm is profoundly modified both by the direct action of the chemico-physical environment in adaptive directions; also as demonstrated by the experimentalists, it is subject to rapid atomic and molecular changes.

Far more important than the decline or senescence of the hypotheses so widely current and so widely debated in 1890 is our new knowledge of the biochemical, bio-

[32] Osborn, 1891: 53.

physical and biomechanical processes which act, react and interact. In this connection may we recall a sentence of my 1890 address: "All the factors of Evolution interact. Variation and Repetition in inheritance are in constant relation with every other factor. Thus we can accumulate facts as to variations *per se,* but if our observation and induction enable us to formulate certain laws, these will always involve at least two factors, *i.e.,* Variation as related to Environment, Variation as related to the life history of individual organisms, Variation as related to Inheritance, Variation as related to Natural Selection."[33]

Our knowledge of the chemical messengers which not only sustain the structural harmonies of the entire organism but which hasten forward some processes and retard others has advanced by leaps and bounds. We are still on the threshold of the biophysical messenger system, but the one fact that certain mammals are sensitive to slight changes in the barometric pressure of the atmosphere which heralds a coming storm is an indication of what we may anticipate in the physical sphere of the interacting messengers.

The hard-won discoveries in aristogenesis which form the chief subject of the present address are entirely the outcome of the spirit of the "interpretation" of nature rather than the "anticipation" of nature, in the language of Bacon the founder of inductive biology. Nature is full of surprises; Nature seldom works according to the anticipations of man, even such semi-inductive anticipations as those of Charles Darwin and of Herbert Spencer. If, as we contend, the principle of Aristogenesis is firmly established by irrefutable paleontological evidence we are now in a new vantage point to attack the problem of the causes of biomechanical adaptations which have interested the mind and excited the imagination of man since the time of Empedocles. Let us summarize our

[33] Osborn, 1891: 53, p. 6.

present position for the direction of further research and experiment.

In biomechanical evolution there are two distinct processes. The one, long known, consists in the alloiometric modification of existing adaptations as in changes of proportion and of function. The other, discovered in course of researches on the phylogeny of the horses, titanotheres and proboscideans, consists in the gradual geneplasmic origin of new and distinct adaptations; it is to the latter originative and creative process that the term Aristogenesis is applied. Both processes become part of the hereditary equipment of the organism.

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ALTERNATION OF SEXUALITY IN OYSTERS

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IN species of mollusks belonging to widely separated groups the sex-differentiating factors have long been known to be in a very labile condition. In both gastropods and pelecypods hermaphroditism is common (Meisenheimer, 1930) and changes of sex often occur as a consequence of age or of environmental conditions. Protandry is of frequent occurrence.

In the genus represented by the oyster, ten species are regularly hermaphroditic (Roughley, 1929), and two of these have been shown to have a more or less regular rhythm of alternating sexual phases (Spärck, 1925, Orton, 1926–'27, Coe, 1931, 1932*a*). Of the fifty other species of the genus *Ostrea* which have been thought to be dioecious it is now known that in each of the three species of which the life histories have been most fully studied many individuals experience at least one functional change of sex.

With the view of obtaining evidence as to the nature of the influences which control these changes in sexuality, studies have been made on one hermaphroditic, larviparous species and one that is seasonally dioecious and oviparous. The California oyster (*O. lurida*) was chosen as a representative of the former group and the American oyster (*O. virginica*) of the latter. Of both species the gonads of young individuals of known ages have been studied at frequent intervals during the development of the primary gonads and through the stages leading to sexual maturity. In *O. lurida* this has included the first three to five sexual phases and in *O. virginica* the first two breeding seasons.

The California oyster appears to be regularly protandric, with a rhythm of female and male phases

repeated in sequence following the preliminary male phase (Fig. 1), but the extent of development as well as the duration of the protandric phase varies to some ex-
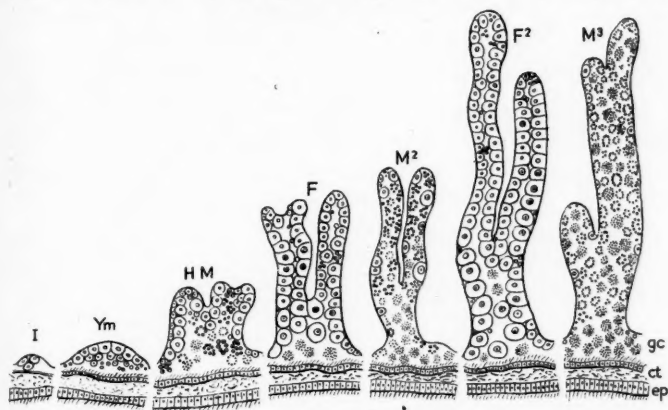
Fig. 1. Diagram showing the sequence of sexual phases in *O. lurida.* *I*, primary indifferent gonad; *Ym*, bisexual gonad, with ovocytes on wall of follicle and spermatogenic cells in lumen; *HM*, first (hermaphroditic) male phase; *F*, extension of follicles and growth of ovocytes in female phase; some sperm-balls remain; M_2, F_2, M_3, second male phase, second female phase and third male phase respectively; *ct*, connective tissue and *ep*, epithelium of body wall; *gc*, genital canal.

tent in individuals of the same age and growing side by side (Fig. 2).

In the American oyster there is a tendency in the same direction (Fig. 3), but in a certain proportion of the young oysters the protandric phase is aborted and such individuals function as females during their first breeding season. The proportion of females among the yearling oysters seems to be fairly constant for a particular locality, for successive samples are in close agreement. In all the localities examined there is always an excess of males in the first breeding season, but the proportion of males is eight to ten times as great in New Haven harbor as it is on the culture floats at West Sayville, Long Island (Table I).

PRIMARY BISEXUAL GONADS

The origin and early development of the primary gonads have been previously described for both species (Coe, 1932a, 1932c). In both, they are well established at the age of twelve to sixteen weeks under normal conditions. In all young individuals they are morphologically similar, containing both ovogonia and spermatogonia. In most cases the spermatogonia proliferate more rapidly than do the ovogonia, giving the early gonad its predominantly male appearance (Figs. 1, 2, 3).
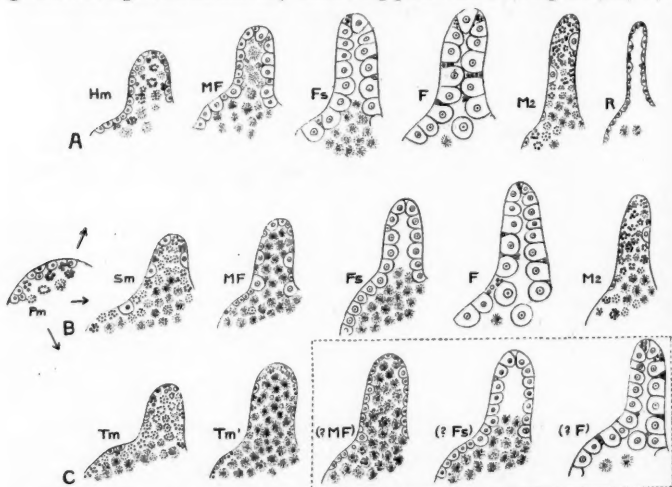
FIG. 2. *O. lurida.* Diagrams showing the sequence of sexual phases following the three types of male phases arising from the primary bisexual gonad (*Pm*); *Hm*, hermaphroditic male with many large ovocytes; *Sm*, secondary male with a few large ovocytes; *Tm*, true male, with no large, but many minute ovocytes; *MF*, transition to first female phase; *Fs*, *F*, first female phase, with many and with few sperm-balls, respectively; *M₂*, second male phase; *R*, recuperation preceding the second female phase. As the diagram indicates, proof is still lacking as to the sexual phases of true males.

From this primary bisexual stage until the development of the functional gametes the gonads of different species, as well as those of the same species in different localities, show much variation in behavior. There is also some variation in different individuals of the same

species in any locality due to the relative rate of growth
of the primary germ cells characteristic of the two sexes.

Although the relative proportion of male and female
cells in the primary gonads forms a graded series, it is
of convenience to distinguish three principal types of
young males (Figs. 2, 3). These may be called, respec-
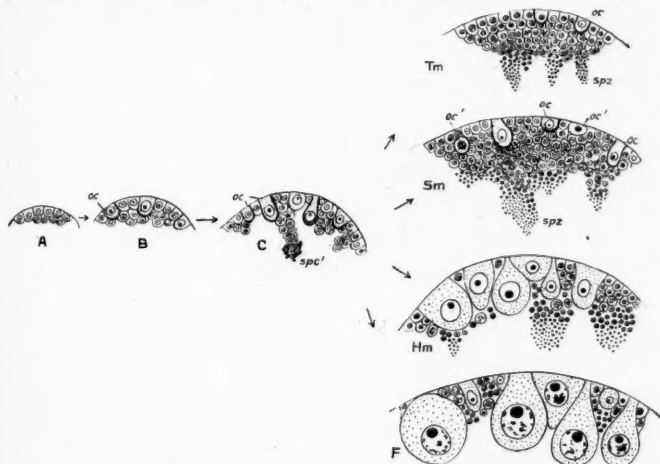
FIG. 3. Diagrams showing the primitive bisexual gonad of *O. virginica*
and its transformation into the definitive spermary and ovary. *A*, early
gonad with undifferentiated cells; *B*, primary bisexual phase, with differ-
entiating ovocytes (*oc*); *C*, later bisexual phase with preliminary abortive
spermatogenesis; *Tm*, true male; spermary with only a few small ovocytes;
Sm, secondary male; spermary with large ovocytes, some of which (*oc'*)
are in process of degeneration; *Hm*, hermaphrodite, with associated spermato-
genesis and ovogenesis; *F*, female; nearly ripe ovary with residual cells and
degenerating spermatocytes; *spz*, spermatozoa.

tively, hermaphroditic males (*Hm*), secondary males
(*Sm*) and true males (*Tm*), although they may represent
only temporary male phases and each may be followed
by a functional female phase. It has not yet been proved
whether these three types are genetically predetermined
or whether, as the evidence now seems to indicate, they
are the responses of a very labile sex mechanism to dif-
ferences in temperature, nutrition or other metabolic
conditions.

Hermaphroditic Males

In *O. lurida* about 85 per cent. of the individuals grow-
ing upon experimental blocks at the pier of the Scripps
Institution of Oceanography at La Jolla, California, form
early gonads that are characteristically hermaphroditic,
with a layer of ovocytes on the wall of each follicle, while
cells in stages of spermatogenesis fill the lumen (Fig. 2,
Hm; Fig. 5, *B*).

In these typically hermaphroditic males the male phase
is of brief duration and the female phase (*F*) immedi-
ately follows the discharge of the relatively few sperm-
balls which such individuals produce. The second male
phase (*M2*) may follow within a few days after the first
ovulation and often while the developing larvae are still
within the mantle cavity of the parent. After a period
of recuperation, if the temperature of the water is suit-
able, the individual assumes the second female phase, to
be followed by the third male phase (Figs. 1, 2). The
number of such phases which may occur in one year de-
pends both upon the season of hatching and the nutritive
conditions of the individual, for the breeding season at
La Jolla may extend over eight or nine months of the
year. If a given individual is hatched in early spring
three of these sexual phases may be completed before the
water becomes too cool for further reproductive activity.
In such cases the second female phase is assumed during
the animal's first winter, but if the individual is hatched
in the summer or early autumn, the sexual phase reached
at the beginning of winter may not be completed until the
following spring. Individuals in all phases of sexuality
may thus be found at all seasons of the year (Coe,
1932a; 1932d).

On the coast of southern New England the approach of
winter checks the development of the primary bisexual
gonad in the young of *O. virginica* before spermatogene-
sis has occurred. The protandric phase is thus aborted,
for no functional spermatozoa are found until the follow-
ing spring. But a small number of spermatids may be

formed as early as November (Fig. 4), when the young
oysters are only four months of age.

At that time there is much variation in the relative size
and abundance of the ovocytes present, but morphologi-
cal sexual differentiation seems to be delayed until the
following spring.   On the south shore of Long Island
and southward a few of the larger individuals show a de-
cided preponderance of ovocytes by the end of November
of their first year, while in a greater number the gonads
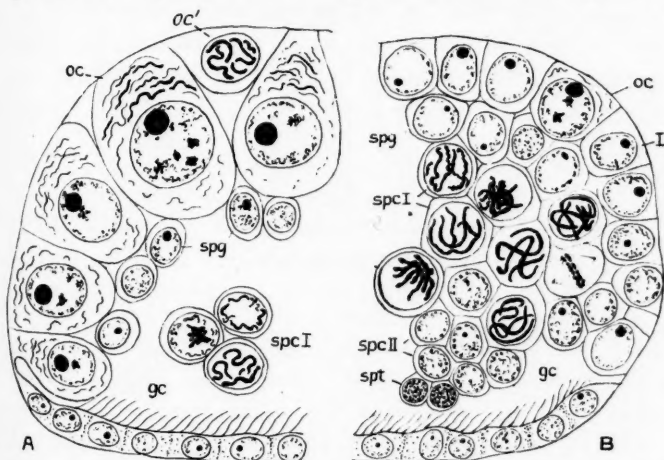
Fig. 4.   *O. virginica*. Portions of two follicles from the same individual
at the age of about four months: one of these (*A*) is predominantly of the
female type, while the other (*B*) consists mainly of spermatogenic cells,
although both show some indications of their bisexual character; *oc, oc'*,
ovocytes, the latter in spireme phase; *spc I, spc II*, spermatocytes; *spg*,
spermatogonia; *spt*, spermatids; *gc*, genital canal.

appear to be predominantly male.   Not infrequently
some of the follicles of the gonads are conspicuously
female in appearance, although other follicles in the same
individual are distinctly of the male type (Fig. 4).   Sam-
ples from Hampton, Virginia, and from Beaufort, North
Carolina, indicate that sexual maturity rarely, if ever,
occurs before the end of the oysters' first winter, even in
those more southern localities.

Little, if any, change is seen in the gonads during the winter, although there may be some degeneration of the spermatids, if any are present. Early the following spring, however, sexual differentiation becomes appar-
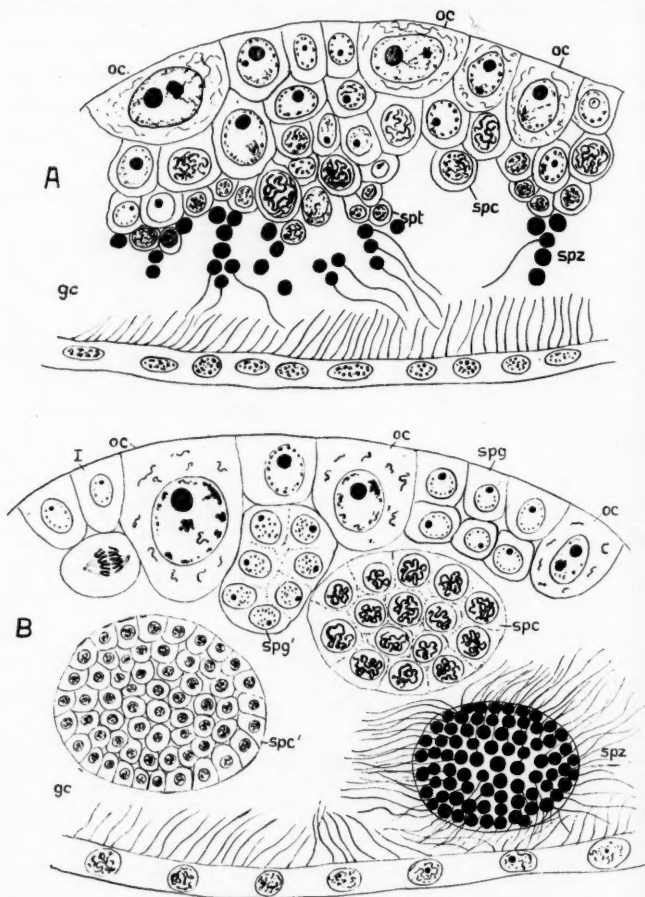
Fig. 5. Portion of biexual gonad in hermaphroditic male of *O. virginica* (*A*) and of *O. lurida* (*B*), showing in each the cortical layer of indifferent gonia (*I*) and ovocytes (*oc*), with spermatogenic cells filling the lumens; *gc*, genital canal; *spc*, *spc′*, primary and secondary spermatocytes; *spg*, *spg′*, primary and secondary spermatogonia; *spz*, spermatozoa (in *O. lurida* united into sperm-balls).

ent, either by the proliferation of the spermatogonia, as is more usual, or by the growth of the ovocytes in the small proportion of individuals which will function as females during their first breeding season.

In only about 1 to 2 per cent. of the total number do both types of cells continue to develop side by side in the same follicle (Fig. 5, *A;* Fig. 6, *B*) or grow in masses in separate follicles. These give rise to functional hermaphrodites in the breeding season. They are evidently comparable with the hermaphroditic males of *O. lurida,* which in that species constitute fully 85 per cent. of the young oysters at the approach of sexual maturity.

Secondary Males

In a small percentage of the young oysters, both in *O. lurida* and *O. virginica,* the growth of many, but not all, of the ovocytes of the primary bisexual gonads is arrested, with a corresponding increase in the number of spermatogenic cells. Spermatogenesis continues in *O. lurida* while the secondary follicles are branching out and the number of sperm-balls is much greater than in the protandric phase of the hermaphroditic males discussed in the preceding section. In these secondary males (Fig. 2, *Sm*) the succeeding female phase (*F*) is long delayed, but it is likewise followed by the second male phase (*M2*).

In *O. virginica* similar males are found. In these the gonads resemble normal spermaries but bear scattered ovocytes on the walls of the follicles (Fig. 3, *Sm*). Many of these ovocytes degenerate before sexual maturity, but others continue to form yolk and may eventually grow to full-sized ova capable of fertilization (Fig. 6, *A*).

True Males

In a still smaller proportion of the young *O. lurida* the growth of all the ovocytes of the primary gonad is inhibited and in many follicles careful search is necessary in order to find even a single small ovocyte. These "true

males'' (Fig. 2, *Tm*) produce even more sperm-balls
than do the secondary males, and the male phase is of
still longer duration. It is not yet known whether the
growth of the ovocytes is later resumed, leading eventu-
ally to the female phase, as in the other two types
of males, or whether successive male phases may follow.

In *O. virginica* the proliferation of spermatogenic cells
to form the spermary is usually accompanied by the ar-
rested development of all the ovocytes present and the
degeneration of some of the others (Fig. 3, *Tm*). But
even in the spermary at sexual maturity the remaining
small ovocytes may be found on the walls of the follicles.
At the close of the breeding season these cells, together
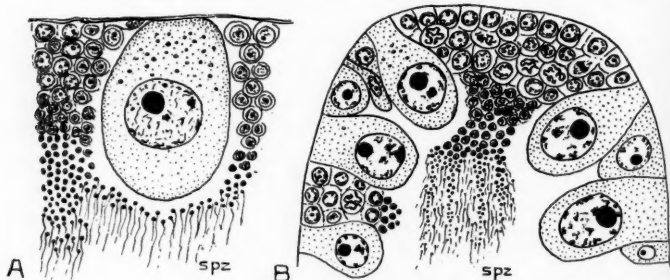
FIG. 6. *O. virginica.* *A*, portion of gonad of secondary male, showing
a single large ovocyte among the spermatogenic cells. *B*, same of hermaph-
rodite, with about equal masses of ovarian and spermatic cells; *spz*,
spermatozoa.

with numerous undifferentiated gonia, are left behind to
form the germinal cells of the following year. In these
residual cells lies the potency of a later change of sex.

FEMALES

The female phase appears only after the primary male
phase in *O. lurida* (Figs. 1, 2), whereas in *O. virginica,*
in the latitude of southern New England, the ovary de-
velops from the bisexual gonad before any spermatozoa
have been formed. The growth of the ovocytes is accom-
panied by the degeneration of such spermatocytes and
spermatids as may be present (Fig. 3, *F*), but many

small ovocytes and indifferent gonia remain as residual cells after ovulation.

Self-Fertilization

In *O. lurida* there is abundant opportunity for self-fertilization, because some of the sperm-balls from the preceding male phase are frequently retained in the genital canals until the female phase is reached and the ova fully grown.

The ova of hermaphrodites in *O. virginica* form apparently normal larvae after self-fertilization, in spite of the great excess of sperm with which they are surrounded.

Sex Ratios

If *O. lurida* is exclusively protandric, with a rhythmical series of alternating sexual phases, the term sex ratio loses its ordinary significance, but if any of the few so-called true males should prove to be strictly genetic males the ratios have still to be determined.

In *O. virginica,* which is seasonally dioecious, with the few exceptions noted in the preceding sections, there is also a strong tendency toward protandry. This is shown by the predominance of males among young oysters at their first breeding season. Local conditions seem to be responsible for the variations in this ratio, for the proportion of females in a colony reared on the experimental floats at West Sayville, Long Island, was much greater than on the natural beds in the bay and eight to ten times as great as in New Haven harbor.

Table I illustrates this fact by comparing the sex ratios during the first breeding season at West Sayville, New Haven and Woods Hole. In the two former localities nearly all individuals become sexually mature and engage in reproduction at the end of their first year, while at Woods Hole the evidence indicates that only about 4 per cent. of the young oysters reach sexual maturity before their second year. At West Sayville about 75 per cent. of the yearling oysters function as males, 23

TABLE I

O. VIRGINICA. SEX AT FIRST BREEDING SEASON

Locality	Im*	M	H	F	Und*	Total
W. Sayville	72**	154	4	48	5	283
New Haven (1932)	17	389	4	13	0	423
New Haven (1933)	0	129	0	7	3	139
Great South Bay	21	197	0	7	0	225
Woods Hole[1]	373	9	3	4	0	389
Woods Hole[2]	3	29	1	16	0	49

* Im, immature; M, male; H, functional hermaphrodite; F, female; Und, sex undetermined; completely spawned.

** All of these would have become sexually mature before the end of the breeding season; reared on culture floats.

[1] At end of first year.

[2] At end of second year; in this locality sexual maturity is usually delayed until the second year of age.

per cent. as females and 2 per cent. as true hermaphrodites capable of self-fertilization, when reared on the culture floats.

At New Haven, on the other hand, about 92 per cent. of the yearling population function as males, 3 per cent. as females, and 1 per cent. as hermaphrodites, while approximately 4 per cent. may remain sexually immature until their second year. At West Sayville the ratio of males to females in the first breeding season is about 100 to 31, while at New Haven it is estimated that there were only 3.3 females to 100 males in the area from which samples were taken in 1932 and about 5 females to 100 males in 1933. From natural beds in Great South Bay there was found about the same sex ratio as at New Haven (Table I).

At the second breeding season there is again an excess of males, but among older oysters it is generally found that the sexes approach equality in numbers, with a slight excess of females in the oldest age groups. This is evidence of either a differential mortality or an actual change in the sex of certain members of the population.

CHANGE OF SEX

The rhythmical sex changes in *O. lurida* have been dis-
cussed in a preceding section. That a functional change
of sex takes place in *O. virginica* has been assumed by
Burkenroad (1931) and others from a comparison of sex
ratios in younger and in older age groups. That it may
actually occur is proved by the experiments of Needler
(1932b), who found that 5 of the 24 surviving oysters
which had been determined as males during one summer
had become functional females the following year, and of
12 females 5 had similarly changed their sex. This is in
harmony with the experiment of Amemiya (1929) on the
Japanese oyster (*O. gigas*) which indicated that about
25 per cent. of the females and 60 per cent. of the males
changed their sex during the interval between two breed-
ing seasons. Roughley (1929) presents evidence that the
Australian oyster (*O. cucullata*) is likewise protandric,
for all except about 5 per cent. of the very young individ-
uals examined by him were males. He found 9 hermaph-
rodites. But among 3,000 large oysters from 30 differ-
ent localities the sex ratio averaged 270 females to 100
males. Two hermaphrodites were found by Amemiya
(1925) in a small collection of the Portuguese oyster (*O.
angulata*) among 14 males and 59 females, but it is not
yet known whether this species is protandric in any por-
tion of its range.

CORRELATION OF SIZE AND SEX

In a strictly protandric species, like the California
oyster, selection of the smallest and youngest individuals
will obviously yield only those that are in the male phase,
but of the three types of males discussed in a preceding
section there is some evidence to indicate that the her-
maphroditic males average somewhat larger than the
other types in which the female phase is longer delayed.
If this evidence is substantiated it will indicate a corre-
lation between the growth of ovocytes and growth of

body or, by inference, between femaleness and favorable metabolism.

In *O. virginica*, however, the evidence is more complete, for it has recently been shown (Needler, 1932*a*; Coe, 1932*c*) that females average much larger than males at their first breeding season. Hence a selection of the largest individuals in a yearling group will include all or nearly all the females. Table II shows that in four sam-

TABLE II

CORRELATION OF SIZE AND SEX IN YEARLING OYSTERS; W. SAYVILLE

	April 29		May 21		June 23		July 29		Total	
Length of shell	M	F	M	F	M	F	M	F	M	F
Less than 50 mm. ...	25	3	21	2	22	1	37	0	105	6
More than 50 mm. ...	5	13	10	6	19	11	15	12	49	42

ples of oysters taken shortly preceding and during the first breeding season there were 49 males and 42 females in the groups having a shell-length of more than 50 mm, while among those of smaller size there were 105 males and only 6 females.

Measurements of a random sample of 402 yearling oysters from New Haven harbor showed a mean length of 31.28 mm for the 389 males and of 38.54 mm for the 13 females. The standard deviation for the males was 6.33, with a coefficient of variability of 20.2, while for the females the corresponding figures were 8.18 and 21.2. A similar sample of 112 individuals from West Sayville showed a mean size of 46.33 mm for the 93 males and 59.33 mm for the 24 females; standard deviation and coefficient of variability were 11.97 and 25.8 for the males and 8.22 and 13.9 for the females, respectively.

Such a correlation may be interpreted as indicating (*a*) that the female is metabolically more active, or (*b*) that she requires more favorable nutritive conditions in order to mature, or (*c*) that the sex factors are in such a labile condition that the metabolism of the individual at

the critical period of sex differentiation actually determines which of the alternative types of cells in the primary bisexual gonads shall predominate. The appearance of the primary gonads seems to be comparable with that of certain races of frogs, in which, as Witschi (1932) has shown, the cortical layer of ovogonia responds to environmental conditions in a different manner than do the spermatogenic cells of the medulla. Favorable metabolism, as indicated by the rate of growth, may tend to accelerate the development of the female cells.

It was mentioned above that local conditions seem to affect the ratio of females to males, for among the yearling oysters on the culture floats at West Sayville the proportion of females is nearly ten times as great as in New Haven harbor. At the former locality the growing season is longer and the average 'length of the shell at the end of the first year is about 50 per cent. greater than at the latter.

The possibilities of local genetic races and differential mortality must also be considered, and it should be recalled that the more numerous males may include a genetically protandric type and a "true" male type, as Orton (1928) has suggested for *Patella*. In *Teredo* likewise a few true males are found among the many protandric females (Coe, *Biol. Bull.*, Vol. 65, 1933).

But since, in general, only the largest oysters develop as females during their first year, with a much greater proportion of females where the nutritive conditions, as indicated by rate of growth, are most favorable it may be tentatively concluded that the sexual conditions are directly influenced by the environment.

The observations (Burkenroad, 1932, and others) that the proportion of males is greater among closely clustered groups than among isolated individuals may indicate less favorable conditions of nutrition at the critical period of sex differentiation rather than any hormonic influence of the associated individuals.

The sexual condition of the individual at the second and later breeding seasons may reasonably be considered as again depending in large measure upon environmental influences, both internal and external, for the gonads after spawning still retain their bisexual potencies. This view is in harmony with the observation that adults of either sex may change to the other, even at the age of several years. That some individuals of *O. virginica* may experience more than one of these seasonal changes of sex during their lifetime seems highly probable, although there is no evidence of a seasonal alternation of sexuality comparable with the sexual rhythm of *O. lurida.*

In both the oviparous and larviparous oysters the sexual sequence or rhythm is interpreted as dependent upon a metabolic rhythm, the expression of which may result from various combinations of genetic factors as well as from varying environmental conditions. The graded series of sexual phases is considered evidence for the quantitative theory of sex.

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INHERITANCE OF THE ELYTRAL COLOR PATTERNS OF THE LADY-BIRD BEETLE, *HARMONIA AXYRIDIS* PALLAS

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INTRODUCTION

THE predacious lady-bird beetle, *Harmonia axyridis* Pallas, belonging to the family Coccinellidae of the Coleoptera, is of very common occurrence in China. Its genetic possibilities suggested themselves by the fact that there is a wide range of variations in respect to its elytral color patterns.

In the summer of 1930 the authors attempted a series of breeding experiments dealing with the inheritance of these variations. A convenient method of describing these variations is from the standpoint of the distribution of black upon a yellow background. A frequent type of beetle has plain yellow elytra without any black (var. *succinea* Hope, Fig. 1, a, c). This type may be taken as the standard type or basis of description. In one series of variations, black appears upon this yellow background in the form of spots, usually rather small, of nearly equal size and distributed as a pattern of symmetrically placed dots on the two elytra. The number of spots varies from one to eight for each elytron (var. *frigida* Muls., Fig. 1, d). A distinct form with nineteen spots (on the two elytra) is called variety *novemdecimsignata* Fald. (Fig. 1, e). A quantitative description of these variations in numbers of black spots was made by the writers and has been reported elsewhere (paper by Tan and Li in press of the Bulletin of the Peking Society of Natural History). At least part of these differences is due to environmental influences, though it seems probable that certain main types have a hereditary basis.

Another series of variations, the so-called "black margined," may be described as the appearance of black at

252

the margin of the elytra, leaving a large yellow area in
the center of each elytron (var. *aulica* Muls., Fig. 1, f).
This black border may be much heavier, leaving only a
small "window" of yellow (var. *conspicua* Muls., Fig.
1, h) or two "windows" (var. *spectabilis* Fald., Fig. 1,
b, g). The results of the preliminary genetic analysis of
the varieties, succinea, aulica, spectabilis and conspicua,
are now presented in this paper.

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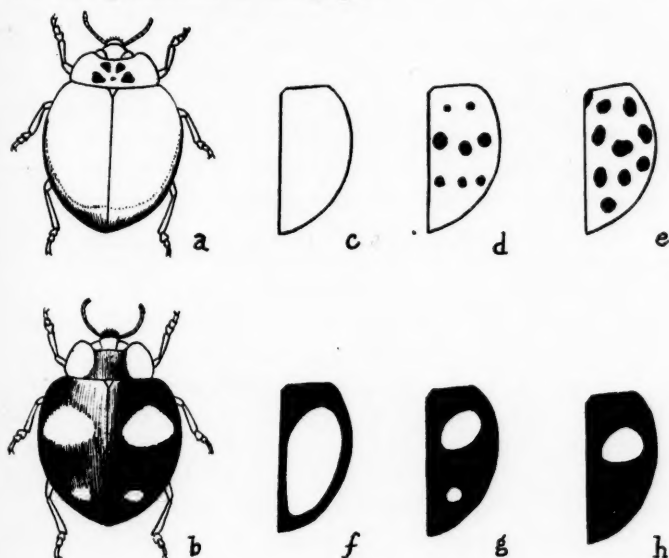
Fig. 1. Beetles and single elytron of *Harmonia axyridis* Pall. (a) Male
with plain yellow elytra (var. *succinea* Hope). (b) Female black margined
with two yellow windows on each elytron (var. *spectabilis* Fald). (c)
Elytron of var. *succinea* Hope. (d) Elytron of var. *frigida* Muls. (e)
Var. *novemdecimsignata* Fald. (f) Elytron of var. *aulica*. (g) Elytron
of var. *spectabilis*. (h) Elytron of var. *conspicua*.

MATERIALS AND METHODS

The beetles may be raised under laboratory conditions
from early April to November, after which time they be-

gin to hibernate. During hibernation most of the speci-
mens can be safely carried through the winter in the lab-
oratory. In the breeding season, they feed exclusively
on aphids. Almost any species of aphids collected wild
or raised in the laboratory will serve the purpose, but so
far no substitute for aphids as food has been found.

Following the conventional approach of genetic inves-
tigation, the writers first attempted to get pure stocks.
Regarding the series with black margined elytra, two
kinds of matings were made, one was the inbreeding of
the one-windowed form, conspicua, and the other, the
two-windowed form, spectabilis. With respect to the
plain yellow and the black spotted elytra, again two sets
of crosses were planned. The one was the inbreeding of
individuals with the maximum number of spots, *i.e.*, var.
novemdecimsignata and the other of those without spots,
var. succinea. Later in the course of the experiment, a
cross between conspicua and succinea gave in F_1 all con-
spicua; attention was then shifted from the homopheno-
typic to heterophenotypic crosses.

Because of the frequent trouble with the aphid supply,
the high mortality rate and the labor demanded in indi-
vidual handling (since the larvae are carnivorous), only
a limited amount of breeding work could be carried on
at a time and a comparatively small number of individ-
uals raised. The different crosses were numbered from
1 to 100; crosses No. 1 to about 20, for instance, were
crosses started early in the season and hence mostly of
P_1 matings, whereas crosses from No. 20 on were of later
matings between F_1 or F_2 individuals. As a means of
making clear the pedigree of certain individuals, other
numbers were given in parentheses to indicate the order
of birth among the offspring of a certain parentage.

The Inheritance of the Yellow and the Black-Margined Elytra

In starting the experiment with beetles collected wild,
the writers could rely on phenotypic characters only, but

these were sharp and easily classifiable. The crosses made in connection with the yellow and black-margined elytra are of three kinds: *viz.*, (A) Plain yellow with yellow (succinea × succinea); (B) two-windowed black-margined (spectabilis) with itself and (C) succinea with spectabilis. To avoid confusion, the results are presented under three separate headings.

A. Yellows crossed with yellows (var. succinea inbred).

Crosses No. 1, 2, 3 and 4 were made with wild beetles having plain yellow elytra. They produced all yellows, as shown in Table 1. For the next generations, five

TABLE 1

PROGENY FROM CROSSES OF YELLOW (SUCCINEA) COLLECTED WILD

Cross	· succinea	
	♀	♂
1	26	26
2	22	23
3	13	16
4	19	22
Total	80	87

pairs of brothers and sisters (crosses No. 21 to 25) were mated, and again only yellows were produced (Table 2).

TABLE 2

PROGENY FROM INTERCROSSES OF F_1 YELLOWS

Cross	Pedigree				succinea	
	♀		♂		♀	♂
21	1	(5)	1	(3)	17	18
22	1	(6)	1	(10)	10	14
23	1	(7)	1	(19)	28	32
24	2	(6)	2	(4)	8	11
25	4	(15)	4	(11)	11	14
				Total	74	89

The inbreeding was carried still another generation: Two crosses (No. 41 and 42) were made from sibs de-

rived from crosses No. 23 and 25, respectively, and again
the progeny were all yellows (Table 3). These crosses

TABLE 3

PROGENY FROM INTERCROSSES OF F₂ YELLOWS

Cross	Pedigree		succinea	
	♀	♂	♀	♂
41	23 (36)	23 (45)	22	12
42	25 (17)	25 (3)	23	12
			Total...... 45	24

establish the fact that all the yellow pairs bred true and
for three successive generations of inbreeding no segre-
gation was observed. This means genetically that the
yellow elytral pattern is a homozygous genotype.

B. Spectabilis crossed with spectabilis.

In contrast to the yellow crosses, matings between
black-margined yielded either black-margined or a mix-
ture of black-margined and yellows. Four crosses (No.
5 to 8) were made, No. 5 and 6 were conspicua and No.
7 and 8 spectabilis. The offspring produced are shown
in Table 4. Cross No. 5 gave 32 conspicua and 5 spec-

TABLE 4

PROGENY FROM INBREEDING OF CONSPICUA AND OF SPECTABILIS

Cross	conspicua			spectabilis			succinea			Ratio
	♀	♂	Total	♀	♂	Total	♀	♂	Total	
5	19	13	32	3	2	5	.....	1	1	.....
6	24	22	46	.....	.....	.....	.....	.....	.....	.....
7	.....	.....	.....	15	11	26	6	4	10	2.89 : 1.11
8	.....	.....	.....	10	11	21	3	2	5	3.23 : .77
				25	22	47	9	6	15	3.03 : .97

tabilis and one succinea male; furthermore, in the next
generation from the mating of conspicua more yellows
were segregated. This complex ratio suggested an in-
teresting relation between conspicua and spectabilis of

the black-margined series which was followed up with results to be discussed later.

Cross No. 6, however, produced nothing but black-margined of the parental type, *i.e.,* conspicua. A brother and sister mating from the offspring of this cross gave 46 individuals (24 female and 22 males) all conspicua. The experiment was carried further into the F_3 generation, resulting in 8 conspicua (2 females and 6 males). As interpreted from the above progeny test for three successive generations, the conspicua in this case likewise were homozygous in genotype.

Crosses 7 and 8, as shown in Table 4, gave together 47 spectabilis and 15 succinea, approximating the ratio of 3 to 1. Among the offspring of No. 7, two pairs of spectabilis sibs (crosses No. 27 and 28) were selected and mated. Both produced nothing but spectabilis, as shown in Table 5. The F_3 progeny which followed in three

TABLE 5

PROGENY FROM INTERCROSSES OF F_1 SPECTABILIS

Cross	Pedigree		spectabilis	
	♀	♂	♀	♂
27	7 (6)	7 (4)	24	19
28	7 (7)	7 (13)	26	21
		Total	50	40

crosses (No. 45, 46 and 47) were again spectabilis (Table 6).

TABLE 6

PROGENY FROM INTERCROSSES OF F_2 SPECTABILIS

Cross	Pedigree		spectabilis	
	♀	♂	♀	♂
45	27 (3)	27 (1)	1	5
46	27 (5)	27 (12)	13	15
47	28 (11)	28 (3)	18	15
		Total	32	35

These facts made it clear that among the black-margined series collected in nature some are homozygous and some are heterozygous for succinea which is recessive to both conspicua and spectabilis.

C. Conspicua crossed with succinea.

Parallel with the all-black-margined and all-yellow crosses, conspicua by succinea crosses were also carried on simultaneously. Three different crosses between conspicua females and succinea males were made successfully. The pedigrees of these pairs were unknown except in No. 9 (Table 7), which was one of the F_2 con-

TABLE 7

PROGENY FROM CROSSES OF CONSPICUA ♀ WITH SUCCINEA ♂

Cross	conspicua			succinea			Ratio
	♀	♂	Total	♀	♂	Total	
9	27	36	63	......	......	......	
10	5	3	8	3	3	6	1.14: .86
11	4	3	7	9	7	16	.61: 1.39
	9	6	15	12	10	22	.81: 1.19

spicua obtained during the preliminary experiment in the fall of 1930 and which had successfully passed the winter. The results of these crosses are shown in Table 7, in which cross No. 9 produced all conspicua and No. 10 and 11 both conspicua and succinea in a ratio approximately 1:1. Apparently the conspicua females used were of 2 kinds: No. 9 female was homozygous, while those in No. 10 and 11 were heterozygous for succinea. Therefore cross No. 9 illustrates a case of P_1 mating with the conspicua character dominant over the succinea and the F_1 offspring all heterozygous for succinea. Crosses No. 10 and 11, on the other hand, illustrate cases of Mendelian "back-crosses," as the 1:1 ratio indicates. In these cases the conspicua offspring are also heterozygous for succinea while the succinea themselves are homozygous.

In order to test out the genetic constitution of these individuals from the above crosses, the following experiments were subsequently carried out. First, the offspring from cross No. 9, which were F_1 individuals, were intercrossed; the results of three such crosses (No. 29, 30 and 31) are given in Table 8.

TABLE 8

PROGENY FROM INTERCROSSES OF F_1 HETEROZYGOUS CONSPICUA

Cross	Pedigree		conspicua			succinea			Ratio
	♀	♂	♀	♂	Total	♀	♂	Total	
29	9 (2)	9 (16)	23	23	46	5	12	17	2.92: 1.08
30	9 (12)	9 (32)	18	10	28	8	2	10	2.95: 1.05
31	9 (87)	9 (3)	19	28	47	12	3	15	3.03: .97
			60	61	121	·25	17	42	2.97: 1.03

As shown in the above table, all of the three cases showed conspicua and succinea segregation in F_2 in an approximately 3 to 1 ratio. There were 121 black-margined and 42 yellows in a total of 163 individuals, with the ratio of 2.97 : 1.03, approaching closely the ideal ratio of 3 : 1.

Second, to confirm that crosses 10 and 11 were backcrosses and that the conspicua progeny were heterozygous for succinea two kinds of tests were made. One was to mate conspicua with conspicua and the other succinea with succinea. The results are shown in Tables 9 and 10 respectively.

TABLE 9

PROGENY FROM INTERCROSSES OF CONSPICUA FROM THE BACK-CROSSES

Cross	Pedigree		conspicua			succinea			Ratio
	♀	♂	♀	♂	Total	♀	♂	Total	
33	10 (5)	10 (10)	7	5	12	....	2	2	3.43: .57
34	10 (44)	10 (39)	16	19	35	5	5	10	3.11: .89
35	11 (21)	9 (15)	32	36	68	20	21	41	2.50: 1.50
36	11 (13)	11 (4)	22	24	46	6	5	11	3.23: .77
Total			77	84	161	31	33	64	2.86: 1.14

TABLE 10

Progeny from Intercrosses of Succinea from the Back-Cross

Cross	Pedigree		succinea	
	♀	♂	♀	♂
37	11 (3)	11 (6)	5	9
38	11 (18)	11 (22)	13	19
39	10 (9)	10 (4)	8	10
Total			26	38

The experiments hitherto described prove conclusively that the yellow character (succinea) is always homozygous and recessive. The heterozygous spectabilis always segregates both the black-margined and the yellows in a typical monohybrid Mendelian ratio, but the conspicua, as indicated in Table 4, may give both spectabilis and succinea segregates. The genetic relationship between conspicua and spectabilis therefore was subsequently analyzed in the following experiments.

The Inheritance of the Different Color Patterns in the Black-Margined Elytra

A. The Genetic Relationship between the conspicua and spectabilis.

It was found in the foregoing experiments that both conspicua and spectabilis could breed true to type and that either one of the two alone could give a 3:1 ratio with succinea. For instance, in cross No. 10 conspicua was used, while in No. 11, the form used was spectabilis. In both cases the respective forms were recovered in the F_2 generation. The question naturally arises as to what is then the relation between the two forms themselves.

In order to analyze the relationship between conspicua and spectabilis, a cross was made (cross No. 12) between a conspicua female and a spectabilis male both collected wild. The offspring produced from such a cross are shown in Table 11 as follows:

TABLE 11

Cross	conspicua			spectabilis			succinea		
	♀	♂	Total	♀	♂	Total	♀	♂	Total
12	25	9	34	9	13	22	8	15	23
Ratio		1.72			1.11			1.17	

As shown in the above table, not only conspicua and spectabilis but also succinea are recovered in the progeny and the ratio is approximately 2:1:1, representing respectively conspicua, spectabilis, succinea. This immediately suggests that spectabilis and conspicua are independent Mendelian characters, and that both are dominant over succinea. Between conspicua and spectabilis there is apparently an "epistatic" dominance in the former over the latter, for when both conspicua and spectabilis appear in the same individual only conspicua character is in evidence, the second yellow spot of spectabilis being covered up by the black pigmentation of the conspicua form. The ratio 2:1:1 further indicates that the parental black-margined were both heterozygous for succinea, for otherwise the yellow character would not be recovered.

In order to check up the genetic constitution of the conspicua and spectabilis recovered on cross No. 12, two intercrosses were carried out, one with conspicua (No. 51 and 52) and the other with spectabilis (No. 53 and 54). Unfortunately cross No. 52 did not yield any offspring. No. 51 gave 7 conspicua (4 females and 3 males) and 2 spectabilis males. The number of progeny is small, but the recurrence of spectabilis from conspicua parents is significant. The results of the crosses No. 53 and 54 (Table 12) more definitely show that the spectabilis and succinea in every case gave a 3 to 1 ratio. These tests show clearly that, while the conspicua form may genotypically be both CS[1] and Cs, the spectabilis forms are

[1] *i.e.* heterozygous for spectabilis.

TABLE 12

PROGENY FROM INTERCROSS AMONG SPECTABILIS FROM CROSS 12

Cross	Pedigree		spectabilis			succinea			Ratio
	♀	♂	♀	♂	Total	♀	♂	Total	
53	12 (22)	12 (29)	24	19	43	1	16	17	2.87 : 1.13
54	12 (33)	12 (23)	14	3	17	1	3	4	3.24 : .76
Total			38	22	60	2	19	21	2.96 : 1.04

invariably S[2] only. The epistatic relation of the two black-margined forms was further confirmed by evidence from another source. Cross No. 5, being a cross between conspicua, produced as seen in Table 4, 32 conspicua, 5 spectabilis and 1 succinea. According to the principle of epistatic dominance, it might suggest the ratio of 12 conspicua : 3 spectabilis : 1 succinea as a result of a cross between two $\dfrac{C}{c}\dfrac{S}{s}$. Selected among the offspring, three different crosses were made: No. 55 was one between spectabilis phenotypes and No. 56 and 57 were between conspicua phenotypes. The result of cross No. 55 is given in Table 13 and those of the two crosses between conspicua in Table 14.

TABLE 13

PROGENY FROM INTERCROSS OF SPECTABILIS FROM CROSS 5

Cross	Pedigree		spectabilis			succinea		
	♀	♂	♀	♂	Total	♀	♂	Total
55	5 (4)	5 (1)	23	18	41	6	9	15
Ratio				2.93			1.07	

The results given in Table 13 furnish additional evidence to what is shown in Table 12. On the other hand the possible ratio that fits the individuals of the different phenotypes in the experiments shown in Table 14 is 12 : 3 : 1, which is to be expected when two heterozygous

[2] *i.e.* homozygous for spectabilis and never heterozygous for conspicua.

TABLE 14
PROGENY FROM INTERCROSS OF COSPICUA FROM CROSS 5

Cross	Pedigree	conspicua			spectabilis			succinea			Ratio
	♀ ♂	♀	♂	Total	♀	♂	Total	♀	♂	Total	
56	5 (2) 5 (14)	10	17	27	4	1	5	1	1	1	13.1 : 2.42 : .48
57	5 (26) 5 (10)	8	3	11	1	1	2	1	...	1	12.57 : 2.29 : 1.14
Total		18	20	38	5	2	7	—	—	2	12.94 : 2.38 : .68

TABLE 15
PROGENY FROM CROSSES HETEROZYGOUS A × A, A × C AND A × S

Cross	Pedigree	conspicua			spectabilis			aulica			succinea			Ratio
	♀ ♂	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	
58 (A x A)	13 (4) 13 (15)							13	8	21	1	7	8	2.9 : 1.1
59 (A x C)	13 (6) 10 (10)	10	9	19				6	4	10	2	1	3	2 : 1.05 : .95
60 (A x S)	13 (3) 9 (16)				39	31	70	27	16	43	17	9	26	2.01 : 1.24 : .75

conspicua with the genetic constitution of $\dfrac{C}{c}\dfrac{S}{s}$ are inter-crossed. Thus all facts point to the conclusion already reached regarding the epistatic relation between conspicua and spectabilis of the black-margined elytra.

B. The Genetic Relationship between conspicua, spectabilis and aulica.

Among the few surviving adults which had hibernated in the laboratory over the winter of 1930, there was one aulica female which had the yellow elytra bordered with a narrow band of black color, as in Fig. 1, f. A cross was made between this female and a succinea male, which was the same parent as in cross No. 9. It produced 8 aulica (6 females and 2 males) and 8 succinea (5 females and 3 males) in exactly a 1:1 ratio (cross No. 13). Inasmuch as this suggested the result of a back-cross, all aulica must have been genotypically heterozygous for succinea. The character aulica is a simple dominant over succinea. In order to test the relation of the character aulica with conspicua and spectabilis the following experiments were performed: The heterozygous aulica (A) females obtained from the above cross (No. 13) were mated with heterozygous aulica, conspicua and spectabilis males respectively. Results of these crosses are presented in Table 15.

The 3:1 ratio obtained from the intercross of heterozygous A (No. 58) shows the expected F_2 segregation of the A character with the succinea; the former, therefore, is proved to be a simple Mendelian dominant over yellow. The results of cross No. 59 between the heterozygous A female and heterozygous C male from cross No. 10, show an approximation of the ratio 2:1:1 in the offspring. This result probably means that C and A are independent characters, with C epistatically dominant over A. Lastly, the cross (No. 60) between the heterozygous A female and heterozygous S from cross No. 9 yields the same results as the above. Therefore S and A are also

independent characters and the former likewise shows epistatic dominance over the latter.

Thus far only these three characters among the beetles with black-margined patterns have been analyzed. The evidence obtained is clear and definite, showing that these three characters are all independent characters, each dominant over the succinea. Among themselves there exists an interesting epistatic series: C is epistatic over both S and A and S over A.

Summary

1. The inheritance of elytral patterns of the lady-bird beetle, *Harmonia axyridis* Pall, was analyzed genetically.

2. The results tend to show that the plain yellow elytron succinea is a simple recessive to any form with black-margined patterns.

3. Among the black-margined beetles, there were three types of patterns analyzed, *viz.*, conspicua, spectabilis and aulica. The genetic results indicate that these characters are each due to an independent Mendelian factor with conspicua epistatic over spectabilis and the spectabilis over aulica in a series.

4. In adapting the symbol A for aulica, S for spectabilis and C for conspicua, the genetic formula for succinea (also for frigida and 19-signata) is therefore aa bb cc; for aulica, AA ss cc; for spectabilis, aa SS cc (or AA SS cc); and for conspicua, aa ss CC (or AA ss CC or aa SS CC or AA SS CC).

THE TWILIGHT SONG OF THE WOOD PEWEE, *MYIOCHANES VIRENS* LINNAEUS

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ONE of the most specialized bird songs is the so-called twilight song of the wood pewee. The bird sings at all hours of the day, but the remarkable twilight song in its most typical form is delivered only at the break of day, and again in the evening near or after sunset. The evening rendition, however, is always a far less perfect piece of continuous and rhythmic music than the dawn song. A few notes characteristic of the dawn song may sometimes be delivered on very cloudy days, but this appears to be an exceedingly uncommon event. The naturalist, Henry Oldys, appears first to have described this distinctive dawn song of the wood pewee, from observations which he made in 1894. Oldys was greatly impressed with the purely musical character of this song and first used the expression "twilight song," applying it, however, to phrase 3 alone. As pointed out by Wallace Craig, the entire composition of which phrase 3 is an element constitutes the twilight song proper. Oldys expressed the opinion that this song was of higher technical rank than that of any other bird song so far as known.

The day song consists of two purely gliding phrases, which may be designated No. 1 and No. 2. No. 1 begins with a certain tone, glides smoothly downward to a lower tone and upward again to cease at a tonal level somewhat lower than the introductory note. The phrase No. 2 begins at about the tonal level of No. 1, glides downward and ceases on its lowest note. It is in reality very nearly equivalent to the first half of the phrase No. 1. These two gliding phrases may be delivered in any order during the brighter hours of the day, but very frequently they are delivered in alternation. The daytime singing

is strikingly lacking in energy and buoyancy, for the drawling phrases are rather listlessly delivered, and long pauses of indefinite length may intervene.
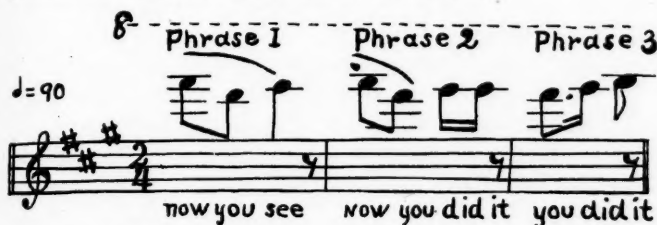
FIGURE 1. Rendering in musical notation the wood pewee's song under observation.

The true twilight song may now be considered. As stated previously, an additional phrase, which may be designated as No. 3, is introduced. This is a non-gliding phrase and consists of three distinct notes stepping up in tonality. While the day song is very leisurely delivered, with perhaps 6 phrases or fewer per minute, the dawn song becomes a rapid continuous rhythmic out-pouring of phrases at the rate of 25 or 30 per minute, for sometimes half an hour. This very distinctive dawn rendition has none of the listless, melancholy character of the usual daytime singing, but becomes a performance bespeaking a mood of tremendous energy and enthusiasm on the part of the little musician. The phrases 1, 2 and 3 are delivered in varying order, and being of such distinctive character afford particularly good material for a detailed analysis of the various arrangements, which seem most natural to the bird.

There is sometimes a further modification in the typical twilight song. The phrase No. 2 may have two additional notes added at the end of the glide, a behavior which was rather consistently followed by the bird whose singing will be subjected to analysis in the present paper. These additional notes were never present in the daytime singing of phrase No. 2, but were rarely absent in the twilight song proper. The rhythm of the three

phrases of this particular bird has always expressed itself to my mind as follows:

Phrase No. 1—Now-you-see
Phrase No. 2—Now-you-did-it
Phrase No. 3—You-did-it

The twilight song may begin at once with phrase No. 3. Usually, however, there is at first a dominance of phrases No. 1 and 2; or a series of these alone may be delivered with some interruptions or pauses. Gradually the pure form of the twilight song is developed, with the maximum number of phrase No. 3 finally introduced. The typical twilight song has then reached its purest expression. Toward the close there is a gradual decrease in the frequency of No. 3 phrases, and these finally are omitted altogether. At this point, the true twilight song impulse has come to an end, and the gliding phrases alone are indulged in briefly.

In July, 1926, the writer observed one particular bird at Lyon Park, Va., recording practically every note delivered at dawn on the dates July 4, 5, 7, 8, 9, 10, 11 and 13. A record of 4,400 phrases was made during this period. Table I expresses the percentage occurrences of the phrases 1, 2 and 3 for the different dates.

TABLE I

PERCENTAGES OF PHRASES 1, 2 AND 3 IN THE SONGS FOR THE
DIFFERENT DATES

Date	Percentage No. 1	No. 2	No. 3	Duration minutes	Rate per minute
1926					
July 4	42.0	19.4	38.23	27	20.2
" 5	35.3	21.3	43.24	30	13.5
" 7	37.0	20.2	42.60	30	18.0
" 8	35.8	21.1	42.90	30	17.8
" 9	30.6	23.4	46.01	26	24.1
" 10	32.6	22.5	44.48	31	24.8
" 11	36.3	21.9	41.66	29	18.2
" 13	32.8	22.3	44.82	18	24.6

The three distinct elements, phrases 1, 2 and 3, may be considered a song unit. It is evident that different permutations of these are possible. In its twilight song the bird makes use of many combinations, as it will be seen. The arrangement 1 3 2 3 1 3 may be considered a typical sequence, since this is actually the arrangement of greatest frequency in the song of the bird observed. Making use of this grouping of six consecutive phrases beginning with every occurrence of phrase 1, a detailed analysis of the 4,400 phrases was made. One thousand four hundred and seventy-three six-note arrangements, beginning with phrase No. 1, were found, involving 85 different combinations. Of this number 68 had one or more occurrences of phrase No. 3, and 17 were composed entirely of the two drawling phrases No. 1 and No. 2 in different arrangements.

The combinations of greatest frequency are arranged in order as follows:

$$
\begin{aligned}
1\ 3\ 2\ 3\ 1\ 3 &= 30.88 \text{ per cent.} \\
1\ 3\ 1\ 3\ 2\ 3 &= 12.42 \text{ '' \quad ''} \\
1\ 3\ 2\ 1\ 3\ 1 &= 11.6 \text{ '' \quad ''} \\
1\ 3\ 1\ 2\ 3\ 1 &= 8.21 \text{ '' \quad ''} \\
1\ 3\ 1\ 3\ 2\ 1 &= 6.11 \text{ '' \quad ''} \\
1\ 2\ 3\ 1\ 3\ 2 &= 4.54 \text{ '' \quad ''} \\
1\ 2\ 3\ 1\ 3\ 1 &= 4.27 \text{ '' \quad ''} \\
1\ 3\ 1\ 3\ 1\ 2 &= 2.98 \text{ '' \quad ''} \\
1\ 3\ 1\ 3\ 1\ 3 &= 2.24 \text{ '' \quad ''} \\
1\ 3\ 2\ 3\ 1\ 2 &= 1.08 \text{ '' \quad ''} \\
1\ 2\ 1\ 3\ 1\ 3 &= 1.08 \text{ '' \quad ''} \\
1\ 1\ 3\ 1\ 2\ 1 &= .95 \text{ '' \quad ''}
\end{aligned}
$$

Of the 1,473 six-note arrangements, 45.6 per cent. showed phrase 3 alternating with every gliding phrase. These involved the three arrangements 1 3 2 3 1 3, 1 3 1 3 2 3 and 1 3 1 3 1 3. As a matter of fact this is the maximum number of arrangements if phrase three always alternates with a gliding phrase.

52.34 per cent. of the six-note arrangements showed phrase No. 3 alternating with gliding phrases, with the exception of a single pair. Typical of this arrangement

is 1 3 2 1 3 1, which in the present analysis occurred with greatest frequency.

Only 2.04 per cent. of the six-note arrangements were composed entirely of the gliding phrases 1 and 2. With few exceptions these were found at the beginning and the closing of the twilight song, and do not represent elements of the true twilight composition.

Some combinations are exceedingly rare, as 1 3 2 1 2 3, since only three instances were found in 1,473 arrangements. In a paper in *The Auk* (Vol. 43, No. 2, April, 1926), Wallace Craig stated that this did not occur in all his records. The combination 1 2 3 1 2 3 occurred only three times in 1,473 arrangements in the song of my own bird. This is of interest, for Craig in the above paper found this often occurring. This would indicate considerable elasticity in the behavior of individual wood pewees in the evolution of their composition. The arrangement 1 3 2 3 2 3 occurred but once in 1,473 instances studied by the writer.

There is strong evidence that certain definite individual patterns of arrangement are dominant in the songs of particular birds. Some arrangements are so infrequent as to indicate an accident of occurrence, or we may say, faulty technique.

It is extremely rare to find two phrases designated No. 3 consecutively delivered. Of 4,400 phrases delivered, one pair of consecutive 3's was delivered on July 4, two pairs on July 10, and one pair on July 11. Even more rarely were two successive 2's delivered, since 4,400 phrases yielded a single pair only on July 4.

An analysis of combinations in groups of three was made to determine those arrangements of greatest frequency. This is shown in Table II.

From these data it is evident that the combination 3 1 3 is the most natural delivery for the bird, the next greatest frequency being 1 3 2.

A count was made of the number of phrases occurring between two sets of combined gliding phrases, where a

TABLE II

PERCENTAGES OF DIFFERENT COMBINATIONS OF PHRASES IN GROUPS OF 3 DETERMINED FOR EACH DATE, AND FOR THE TOTAL OF 4,400 PHRASES DELIVERED FROM JULY 4 TO JULY 13 INCLUSIVE

Date July	Total phrases	313 %	132 %	231 %	131 %	323 %	213 %	321 %	312 %	123 %	121 %	112 %	211 %	311 %	111 %	113 %	212 %	133 %	331 %	332 %	212 %	221 %	122 %
4	545	19.3	10.5	7.7	17.4	3.3	8.4	7.7	5.5	5.0	2.0	2.4	1.1	1.5	1.1	.9	.2	.2	.2	—	.2	.2	.2
5	407	21.4	17.4	11.8	12.5	9.3	8.9	8.4	2.9	2.0	1.0	.2	.2	.2	.2	.2	.5	.5	.5	—	.5	.2	—
7	543	22.7	14.2	13.1	15.1	8.7	5.5	5.3	5.3	4.2	1.7	.6	.9	.5	.2	.7	.2	—	—	—	.2	—	—
8	535	21.9	16.8	12.7	13.1	9.5	7.7	7.5	3.2	3.0	.9	.4	.3	.6	.6	.3	.4	—	—	—	.4	—	—
9	627	23.4	20.6	18.8	6.9	15.8	4.0	4.2	2.2	1.9	.5	.3	.3	—	—	.1	.2	.2	—	—	.2	—	—
10	771	20.8	18.6	15.6	8.0	13.8	5.6	5.3	2.3	2.2	.8	.6	.6	.4	.5	.3	—	—	.3	.3	—	—	—
11	528	20.1	15.0	14.4	12.3	9.1	6.8	5.9	5.7	5.3	1.7	.6	.6	.6	.6	.4	.2	.2	—	—	.2	—	—
13	444	21.9	19.4	16.7	8.8	14.6	5.4	5.0	2.7	2.0	.9	.2	.2	.5	.9	.2	.2	—	—	—	.2	—	—
Total*	4400	21.4	16.6	14.0	11.5	10.7	6.4	6.0	3.7	3.3	1.1	.7	.6	.5	.5	.4	.2	.1	.07	.05	.2	.02	.02

* The final percentages are not summations of percentages determined for each date but actual calculations of the total number of occurrences for each combination in relation to the total number of phrases, *i.e.*, 4,400.

gliding phrase always alternated with No. 3. The maximum number found was 53; this occurred but once in 4,400 phrases. There occurred the following arrangement: *2 1* 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 1 3 2 3 1 3 2 3 1 3 *2 1*. The greatest frequency was found where only three phrases intervened between two pairs of gliding phrases. It would seem that this outpouring of 53 phrases, in which a gliding phrase always alternated with phrase 3, represents the purest expression of the typical twilight song of the wood pewee.

From the preceding discussion and analysis of the main features of the twilight song, one must admit that this is a most remarkable composition. It is remarkable because certain elements of fixity characterize its composition. In some features it is decidedly mechanical with respect to the percentage composition of various of its elements.

In the song of my particular wood pewee, about 43 per cent. of its phrases were 3's, and this figure was very closely approximated on every day its song was observed. Craig has found that some individuals introduced as low as 25 per cent. of 3's into their song, while others gave as high as 57 per cent. Whatever the percentage may be, this particular feature appears to be a rather stable element of its song pattern.

If the gliding 1's and 2's always alternated with 3's in the typical twilight singing, both would show a 50 per cent. occurrence. If the percentage falls below 50 per cent., there must be a greater proportion of successively delivered gliding phrases. If more than 50 per cent. of 3's is introduced into the song, it must follow that many 3's will be consecutively delivered. In the case of my own bird it has been seen that a consecutive delivery of 3's is very rarely indulged in and at no time were more than two consecutively delivered.

It is obvious that certain arrangements of 1's, 2's and 3's are much more freely and naturally delivered than

others, the arrangement 1 3 2 3 2 3, for instance, occurring but once in 1,473 six-phrase groups beginning with phrase No. 1. There are probably sound physiological reasons for these common and these uncommon arrangements; in the case of the latter some are so rarely indulged in as to appear purely accidental. On the whole I would pronounce the bird a rather mechanical singer, with rather definite percentages of phrases and verses, so to speak, associated with its physiology. Individuals sing only approximations of the same tune, it would seem, and the feature of alternation between the gliding and the non-gliding phrases, *i.e.,* the 3's, is a variable one. Since the bird introduces non-gliding 3's only into its twilight composition, and successive 3's are rarely delivered, I am inclined to believe that its most perfect musical technique is shown when the glides, either 1's or 2's, alternate with the non-gliding 3's.

WOOD PEWEE'S SONG, JULY 10, 1926

(Began 4 A.M.; ended 4: 30 A.M.; 771 phrases delivered)

2 pause 1 pause 1 1 1 2 1 3 1 2 3 1 1 3 1 3 2 1 3 1 3 2 1 3 1 3 2 1 3
1 3 2 1 3 1 3 2 3 1 3 2 1 3 1 2 3 1 3 1 3 2 3 1 3 1 3 2 1 3 2 3 1 3 1 3 2
1 3 1 3 1 3 2 3 1 3 1 3 2 3 1 3 1 3 2 1 3 1 3 2 1 3 1 2 3 1 3 1 3 2 3 1
3 1 2 3 1 3 2 1 3 1 3 2 3 1 2 3 1 3 2 1 3 1 2 3 1 3 2 3 1 3 2 1 3 2 1 3
1 3 2 3 1 3 2 3 1 3 2 1 3 1 3 2 3 1 3 1 3 2 3 1 3 1 2 3 1 3 2 3 1 3 2 3
1 3 2 3 1 3 2 1 3 2 3 1 3 2 1 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 1 3 2
3 1 3 2 3 1 3 2 3 1 3 1 3 2 1 3 1 3 2 3 1 3 2 1 3 1 3 2 3 1 3 2 3 1 3 1
3 2 3 1 3 2 1 3 2 3 1 3 1 3 2 3 1 3 1 2 3 1 3 2 3 1 3 2 1 3 2 1 3 1 3 1 3
2 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 1 3
2 3 1 3 1 3 2 3 1 3 2 1 3 1 3 2 3 1 3 1 2 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2
3 1 3 1 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 1
3 2 3 1 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3
2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3
1 3 1 3 2 3 1 3 1 3 2 3 1 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 1 3 1 3 2 3 1 3
2 3 1 3 2 3 1 3 2 1 3 3 2 3 1 3 2 3 1 3 2 3 2 3 1 3 2 3 1 3 2 1 3 1 3 2
3 1 3 2 1 3 1 3 2 6 1 3 2 3 1 3 2 3 1 3 2 3 1 3 1 3 2 3 1 3 2 3 1 3 1 3
2 3 1 3 1 3 2 3 1 3 2 1 3 1 3 2 1 3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 2 3 1
3 2 3 1 3 2 3 1 3 2 3 1 3 2 3 1 3 1 pause 2 3 1 3 2 3 1 3 3 2 1 3 1 3 2
3 1 3 2 3 1 2 3 1 3 2 3 1 3 2 3 1 3 2 1 3 2 3 1 3 2 3 1 3 1 3 2 3 1 3 2
1 3 2 3 1 3 1 3 2 3 1 3 2 3 1 3 2 1 3 1 3 1 3 2 3 1 3 2 1 3 1 3 2 3 1 3
2 3 1 3 1 3 2 1 pause 2 pause 3 1 3 1 3 1 pause 2 1 pause 1 3 1 2 3 1
pause 1 2 1 3 2 1 3 1 2 3 1 3 1 2 3 1 pause 1 2 3 1 3 1 2 (4: 30 A.M.)
1 3 1 2 3 1 2 (4: 31 A.M.) 1 1 1 2 1 1 1 (singing ceases).

One may ask why this distinctive composition is confined to the twilight period of dawn and evening. It is my opinion that it is purely a response to certain levels of light intensity, for it appears to begin at a certain intensity level and ceases when the dawn light has advanced to a certain point. Why this should affect the bird's musical impulses as it does, leading to the introduction·of distinctive sounds delivered at no other time, is not clear. It is known, however, that a number of the flycatchers respond to dawn and evening twilight with unusual musical composition; the kingbird also being one of these.

SHORTER ARTICLES AND DISCUSSION

AN ANALYSIS OF SIZE GENES

In an earlier study the writer (1931) presented evidence of the association of greater adult weight with brown coat color in the back-cross generation of a mouse interspecific cross. This back-cross was produced by mating large *Mus musculus* females carrying the recessive color genes for dilution (d), brown (b) and non-agouti (a) to F_1 males from *musculus* dams and *Mus bactrianus* sires. Since the small race of *Mus bactrianus* possesses the corresponding allelomorphs (DBA^w), the back-cross generation permitted the detection of any association between size and color. A subsequent report (1933) supplied confirmatory data from the F_2 generation. In an investigation now in progress, the same trend is evident in two additional types of back-crosses in which reciprocal F_1 females are mated to *musculus* males. The interpretation that factors influencing size (weight) are found on the chromosome with the gene for brown coat color in the cross between these two strains of mice seems to be well substantiated by an abundance of data.

The 1931 study likewise showed association between brown coat color and several additional size characters, including body length and humerus, femur and tibia lengths. If the larger average size of these characters, as well as of weight, in brown mice is a manifestation of the influence of general genes affecting growth in all parts of the body, the evidence is conflicting, for still other quantitative characters, especially skull (interorbital) width and tail length, show such an association, if at all, to so slight an extent as to be of no significance. Evidence derived from a study of foot length in both back-cross and F_2 generations (Green, 1933a) is strongly suggestive of the presence of factors of the type termed by Wright (1932) "group" factors, influencing the bones of the hind limb, on the b chromosome. Since, in general, brown back-cross animals tend to exceed blacks in all quantitative characters investigated, excepting only cranial capacity in both sexes, skull width in females (with the means the same) and tail length in males (with the black mean slightly greater than the brown), although not significantly in all, it seems possible that more than one type of gene or group of genes

275

influencing size may be situated on the b chromosome.   The 1931 data permit some analysis of this point.

Of the quantitative characters exhibiting linkage with brown, as determined by a difference between the means of brown and black back-cross animals as great as or greater than 4.0 times its probable error, 181st day weight (W), body length (B), femur length (F) and tibia length (T) are selected as representative. Of these, weight is obviously a manifestation of general size. Body length may be assumed, *a priori*, likewise to be largely a manifestation of general size, although perhaps to a lesser extent than weight, while the lengths of femur and tibia may or may not be.

If femur and tibia length are not entirely functions of general size, they should be correlated more highly together than is either with weight or body length.   Similarly, if weight and body length are largely the end results of common factors, they should show a higher degree of correlation with each other—all else being equal—than does either with femur or tibia.   The intrinsically variable nature of weight, in which fluctuations in amount of food ingested and degree of obesity play a part, and to a lesser extent the lack of precision in obtaining body lengths (which were measured to the nearest mm only), militate against as accurate a determination of the relationship between them as can be obtained for the two leg bones, amenable to exact measurement, even though fundamentally the two pairs of variables were equally closely associated in development.

Second order correlations, in which two variables are correlated with the other two held constant, are well suited for measuring relationship.   These were computed according to the standard formula:

$$r_{12\cdot34} = \frac{r_{12\cdot3} - r_{14\cdot3} \cdot r_{24\cdot3}}{\sqrt{1 - r_{14\cdot3}{}^2} \sqrt{1 - r_{24\cdot3}{}^2}}.$$

The coefficients of correlation are listed in Table 1.

In all correlations, 150 males and 137 females were involved.

The results in Table 1 bear out our postulations and indicate that femur and tibia are influenced by common factors independent of those influencing weight and body length, which latter in turn may likewise be affected by factors other than those bearing on the leg bones.

Since weight, body length, femur length and tibia length are influenced by genes on the b chromosome the question follows as

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TABLE 1

SECOND ORDER CORRELATION COEFFICIENTS FOR QUANTITATIVE
CHARACTERS

</div>

Subscript	Coefficient
WB.FT	♂ + 0.3781 ♀ + 0.5775
WF.BT	♂ + 0.1433 ♀ + 0.0618
WT.FB	♂ − 0.0195 ♀ + 0.0905
BF.WT	♂ + 0.2199 ♀ + 0.4696
BT.WF	♂ + 0.2830 ♀ + 0.0526
FT.WB	♂ + 0.6270 ♀ + 0.6779

to whether the same genes are responsible for the observed effects in all four characters or whether, on the other hand, both "general" and "group" genes are located on the one chromosome. Indirect methods may give a clue to the situation.

Introducing third order correlations, in which those of zero order involving color (black, brown) are ordinary product-moment correlations, we find for males: $r_{WB.FTC} = +0.3754$, and $r_{FT.BWC} = +0.6274$; for females: $r_{WB.FTC} = +0.5886$ and $r_{FT.BWC} = +0.6689$. When compared with the corresponding second order correlations in Table 1, it is evident that color (the allelomorphs, black and brown) has little effect independently on weight or body length, and femur or tibia lengths.

If weight and body length are affected jointly by the same genes and femur and tibia similarly by other genes, $r_{WB.C}$ and $r_{FT.C}$ should be less different from r_{WB} and r_{FT}, respectively, than weight and femur, for example, correlated with other characters, since, in general, the excess difference should be largely due to crossing-over between our postulated general genes linked with brown and the group genes on the same chromosome. Table 2 presents the figures obtained.

The greater differences between the members of pairs 2 and 3 in Table 2 over the corresponding differences in pairs 1 and 4 are not antagonistic to the possibility that the b chromosome has

TABLE 2

ZERO AND FIRST ORDER CORRELATIONS

Subscript	Males		Females	
	Coefficient	Difference	Coefficient	Difference
(1) WB	+ 0.5726	0.0254	+ 0.7137	0.0163
WB.C	+ 0.5472		+ 0.6974	
(2) WF	+ 0.4802	0.0422	+ 0.5153	0.0497
WF.C	+ 0.4381		+ 0.4656	
(3) WT	+ 0.4325	0.0336	+ 0.4500	0.0449
WT.C	+ 0.3989		+ 0.4051	
(4) FT	+ 0.7902	0.0118	+ 0.7988	0.0174
FT.C	+ 0.7784		+ 0.7814	

genes influencing the leg bones independently of weight and body length and also others influencing the two latter characters. Although the differences in themselves are slight, the trend is constant. The inference that both "group" and "general" factors are present seems logical.

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A NEW SEX–LINKED, FEMALE–LIMITED LETHAL OF DROSOPHILA MELANOGASTER

A NEW sex-linked, female-limited lethal called lw, and killing only females homozygous for it, made its appearance in the third generation following a cross of ebony male by wild type female. The sex ratios in the three successive generations were: 74 ♂ : 65 ♀; 115 ♂ : 102 ♀; and 126 ♂ : 71 ♀. All flies of the last bottle (from ebony ♂ by grey ♀) were of the wild type.

The presence of the lethal can not be recognized by its effect on either sex in the imago, which is in contrast to the case of D. H. Thompson (1921), who described a lethal whose presence in the male could be noted by its effect on the wings and legs. Emergence of flies from pupae isolated in various stages of development indicates that the lethal is effective in either larval or egg stages.

The abnormal ratio was followed through eight generations. Of 57 matings in which both male and female came from bottles bearing the ratio of 2 ♂ : 1 ♀, 32 gave the normal and 24 the ratio of 2 ♂ : 1 ♀, including one doubtful case with 156 ♂ : 102 ♀. This deviates from expectation for a 2 ♂ : 1 ♀ sex ratio by 2.1 times the standard error, but 3.4 times the standard error for a 1 : 1 sex ratio. The remaining bottle yielded 38 ♂ : 85 ♀, and was probably the result of an ordinary sex-linked lethal. A summary of these matings is given as follows:

Ratio	No. ♂	No. ♀	Per cent. ♂	Per cent. ♀	No. of matings
2♂ : 1♀	3142	1604	66.2	33.8	24
1♂ : 1♀	2150	2227	49.1	50.9	32
1♂ : 2♀	38	85	30.8	69.2	1

Graph I indicates the distribution of the percentages of males from matings of ♂ by ♀ coming from bottles with the 2 ♂ : 1 ♀.

The matings which produce 2 ♂ : 1 ♀ can be represented as follows on the assumption that the lethal is sex-linked: $\frac{lw}{+} \times \frac{lw}{Y}$ $\left(\frac{lw}{lw}\right) + \frac{lw}{+} + \frac{lw}{Y} + \frac{+}{Y}$. One half of the matings from such a bottle should repeat the ratio of 2 ♂ : 1 ♀, while the remainder should give the normal ratio, which agrees with the results. The homozygous lethal lw females are of course eliminated. A ratio of 2 ♂ : 1 ♀ could be obtained from an autosomal factor lethal only for females, but in the next generation matings with 2 ♂ : 1 ♀ *and* 4 ♂ : 3 ♀ ratios would be obtained. There is no indication of the latter ratio.

Of eleven matings of males from non-lethal stocks by females from bottles giving 2 ♂ : 1 ♀, ten gave normal sex ratios and the eleventh showed a ratio of 39 ♂ : 80 ♀. This, as in the case above may have been due to an ordinary sex-linked lethal gene. Of

88 F_2 bottles from the above-mentioned matings, 21 showed a clear ratio of 2 ♂ : 1 ♀ and 60 gave clear 1 : 1 sex ratios. Two are doubtfully considered as 2 ♂ : 1 ♀ (171 ♂ : 112 ♀ ; 117 ♂ : 75 ♀), and five gave rather extreme deficiencies of males (70 ♂ : 100 ♀ ; 98 ♂ : 134 ♀ ; 107 ♂ : 183 ♀ ; 30 ♂ : 66 ♀ ; 16 ♂ : 32 ♀). The latter were probably due to an ordinary sex-linked lethal gene, and were not included in the mean. Graph 2 shows the relationship of percentages of males from those F_2 bottles. According to expectation 25 per cent. of the F_2 bottles would give a ratio of 2 ♂ : 1 ♀. Actual results show 26.7 per cent. of bottles throwing this sex ratio.

Further evidence that the lethal factor is present neither in the second nor third chromosome was obtained from crosses in-

Graph 1. Distribution of percentage of males from matings of males by females throwing a ratio of 2♂:1♀.
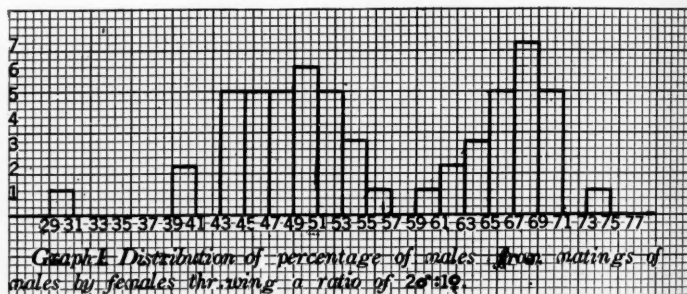
volving lobe and ebony respectively: (1) in F_2 from lobe ♂ by heterozygous lw female the percentage of wild was 28 per cent. in bottles showing 2 ♂ : 1 ♀, approximately the 25 per cent. expected from random assortment; and (2) in F_2 from ebony ♂ by heterozygous lw females 24 per cent. of the flies were ebony in bottles showing 2 ♂ : 1 ♀, again in agreement with expectation under random assortment.
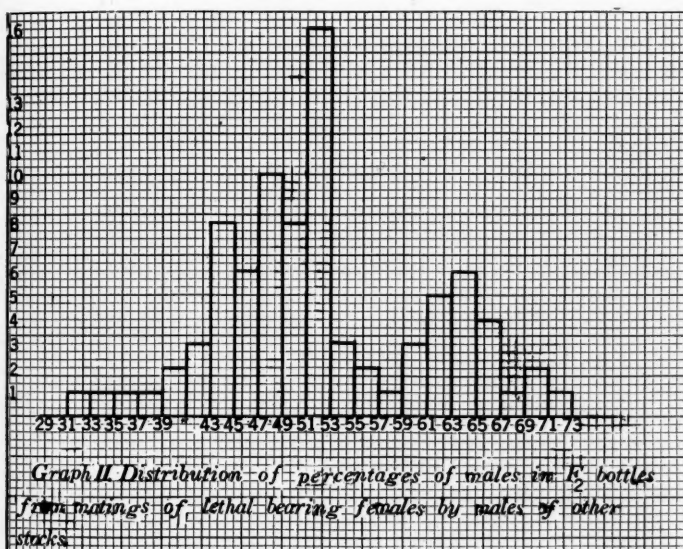
Of 24 F_2 matings from Bar ♂ by heterozygous lw females only two gave the ratio of 2 ♂ : 1 ♀ with a total of 14 crossovers to 135 non-crossovers:

Males		Females	
B	+	B	+
175	123	135	14

The per cent. of crossovers is 9.4 with a standard error of 2.6.

In other cases heterozygous lw females were mated with males of eosin-miniature stock. The F_1 bottles gave normal sex ratios, but ratios of $2\,\male : 1\,\female$ were recovered in some of the F_2 bottles. Matings were made between eosin-miniature males and their sisters from such bottles. In those which gave $2\,\male : 1\,\female$ in the F_3, the males must have been $\dfrac{w^e mlw}{Y}$ but the females might be of

any one of four types: $\dfrac{w^e m +}{+ + lw}$, $\dfrac{+ m +}{+ + lw}$, $\dfrac{w^e + +}{+ + lw}$ or $\dfrac{+ + +}{+ + lw}$. Of

Graph II Distribution of percentages of males in F_2 bottles from matings of lethal bearing females by males of other stocks

twelve bottles with $2\,\male : 1\,\female$, six turned out to be type $\dfrac{w^e mlw}{Y}$ by $\dfrac{w^e m +}{+ + lw}$ and the other six were of the type $\dfrac{w^e mlw}{Y}$ by $\dfrac{+ m +}{+ + lw}$.

	6 bottles			6 bottles	
	$\male$	$\female$		$\male$	$\female$
Type	273	80	Type	413	162
eosin-miniature	242	168			
eosin	115	19			
miniature	140	102	miniature	431	290

The percentage of recombination between eosin and the lethal was 49.3, indicating extreme separation. Eosin and miniature show 32.8 per cent. recombination. Between miniature and the lethal recombination occurred 26.8 per cent. of the time in the first group of bottles and 35.8 per cent. of the time in the other group, an average of 31.8 per cent. As Bar at locus 57 is only 21 units beyond miniature, these data clearly indicate that the lethal is beyond Bar and approximately at locus 66.

Other sex-linked, female-limited lethals are comparatively rare in the literature. The only other cases known to us are D. H. Thompson's (1921) lethal-erect (locus 38), and Bonnier's (1923b) lethal g (locus 63.1). It is possible that our lw is the same as Bonnier's lg.

The absence of the lethal effect in males in these cases suggests the presence of normal allelomorphs in the Y chromosome, and the proximity of lg and lw to bobbed (locus 70), demonstrated to have such a normal allelomorph, suggests that there may be a section of several units carrying normal genes in this region of the Y chromosome. On the other hand, Morgan, Bridges and Sturtevant have listed two ordinary lethals (lethal 18, locus 67 ± and lethal sc, 66.2) as well as the gene bordered, which do not have normal allelomorphs in the Y-chromosome.[1]

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SEED FREQUENCIES IN *CYTISUS* AND *PELTANDRA*[1]

THE object of this paper is to present new estimates of seed frequency in the seed pods of *Cytisus scoparius* Link. and in the fruits of *Peltandra virginica* Kunth. and to compare the statistical constants describing these distributions with the previously published data for these species. In the first case we are dealing with a species that was introduced into Massachusetts about 75 years ago; the counts of Pearson (1901) are based on pods taken from plants grown in England, and those of Harris (1909) concern plants growing in Massachusetts. The close agreement of their results indicates that in this case an introduced species is no more variable in its new habitat than in its old one. It seemed of interest to make another estimate of the seed frequency in this species to see how persistent this agreement might be and in order to see how closely the measures of deviation previously recorded would apply to another sample. Accordingly, on July 1, 1933, seed pods were collected from a patch of *Cytisus* growing near the water's edge a short distance northwest of the Marine Biological Laboratory at Woods Hole, presumably from the same plants from which Harris collected his samples 26 years earlier. Approximately the same number of pods were taken from each bush in the patch; the number of seeds in each of the 329 pods was counted, and from these data the mean and standard deviation and their probable errors and the coefficient of variation were calculated. These constants, and those of Pearson and Harris, appear in Table 1; the three sets of constants stand in very good agreement with one another.

The actual frequency distribution of the seeds of this sample agrees closely with the two other reports, and since it is based

TABLE 1

COMPARISON OF STATISTICAL CONSTANTS FOR SEED DISTRIBUTION IN
Cytisus PODS

	Mean	Standard deviation	Coefficient of variation
Danby Dale, England...	$9.643 \pm .069$	$3.547 \pm .048$	$36.78 \pm .57$
Woods Hole, 1907.........	$9.998 \pm .050$	$3.524 \pm .035$	$35.24 \pm .40$
Woods Hole, 1933.........	$9.787 \pm .129$	$3.468 \pm .091$	35.44 ± 1.04

[1] From the Department of Biology of the School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland.

on smaller numbers of pods than the other two there is no need to present it here. The seeds were not quite fully formed at the time this collection was made and it was the intention to take a larger sample later, but the seed pods became infested with beetles and fungi subsequently and it was impossible to make another count.

Peltandra virginica, a member of the Araceae, bears heads containing 15 to 65 fruits, which in samples taken in Maryland range in color from green to dark reddish brown. These fruits may be seedless, in which case they are small and shrunken, or they may contain one, two or, rarely, three seeds which are globular, and nearly a centimeter in diameter. In an earlier paper, which was principally concerned with the ability of these seeds to germinate in the absence of oxygen, the frequency distribution of *Peltandra* seeds in a collection made along the Potomac River in Maryland in 1932 was presented and discussed, and certain papers dealing with seed distribution were reviewed (Edwards, 1933). In this sample seedless fruits were not recorded. Since then two other collections of *Peltandra* fruits have been studied in this way. A sample of 30 *Peltandra* heads grown in the Botanical Garden of Smith College at Northampton, Massachusetts, containing reddish brown seeds, was made available through the courtesy of Dr. Dorothy Day. The mean number of fruits per head was 45.1 ± 1.1, the standard deviation $9.32 \pm .81$, and the coefficient of variation 20.7 ± 1.9. Another sample of 67 heads was obtained in a swamp south

TABLE 2

SEED DISTRIBUTIONS IN THREE SAMPLES OF *Peltandra virginica* FRUITS AND THEIR STATISTICAL CONSTANTS

Seeds per fruit		Frequency			
		0	1	2	3
Maryland,	1933	519	2013	120	2
Massachusetts,	1933	585	766	6	0

		Number of seeds per fruit		
		Mean	Standard deviation	Coefficient of variation
Maryland,	1933	$0.853 \pm .011$	$0.370 \pm .003$	43.4 ± 4.4
Massachusetts,	1933	$0.573 \pm .010$	$0.412 \pm .005$	71.9 ± 6.0

of Annapolis, Maryland, on September 30, 1933, in which the mean number of fruits per head was $39.6 \pm .8$, the standard deviation $9.88 \pm .57$ and the coefficient of variation 25.2 ± 1.6. The frequency of occurrence of seedless, one-, two- and three-seeded fruits is given in Table 2.

In each of the three series one-seeded fruits were found more frequently than any of the other classes, two-seeded fruits occurred relatively infrequently and three-seeded fruits were still more uncommon. Next to the one-seeded fruits in frequency were the seedless fruits, which amounted to 43.1 per cent. of the total number of fruits in the Massachusetts sample and 19.5 per cent. in the Maryland sample taken in the same season. It appears that *Peltandra* plants did not find as favorable conditions for seed production in the more northern habitat, and this is borne out by the lower proportion of two-seeded fruits (0.44 per cent., as compared with 4.53 per cent. in the Maryland sample) and the absence of three-seeded fruits. This is further shown by the mean number of seeds per fruit in the two samples presented in Table 2.

The heads that produced the 2 three-seeded fruits found in the 1933 Maryland sample were characterized by high fertility in all their fruits. One head bore 49 fruits in all, of which only 2 were seedless, 31 had one seed, 15 were two-seeded and one fruit had three seeds. The other head containing a three-seeded fruit had 6 seedless fruits, 13 one-seeded ones and 14 with two seeds. Two-seeded fruits were far more numerous in these two heads than in the rest of the sample.

Summary

The seed distribution in a sample of *Cytisus scoparius* pods was found to be the same as that observed by earlier workers. Similar counts for *Peltandra virginica* fruits showed the one-seeded fruits to be most numerous, as previously reported, and indicated that there was a larger proportion of fertile fruits in a sample collected in Maryland than in one from Massachusetts.

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THE RELATIVE EFFICIENCY OF TWO METHODS OF MEASURING HUMAN LINKAGE

Bernstein (1931) devised a method for detecting and measuring linkage in man when only two generations are available. Wiener (1932) has devised an alternative method. Owing to the difficulty of obtaining human data it is clear that they should be treated so as to extract as much information as possible. It is therefore desirable to compare these two methods.

Let c be the recombination value for the two genes whose linkage is under investigation, and let $x = c - c^2$. Let s be the size of the family investigated and n the number of families. We confine ourselves to the simplest case, where there is no ambiguity in the classification of the genotypes. This is the mating $AaBb \times aabb$ and reciprocally, or in the pedigrees now available, such matings as $AB + + \times O + -$, where AB and O refer to blood groups and the two following signs to the presence or absence of the agglutinogens M and N. The expectation is either

> *(1−c)AaBb: c Aabb: c aaBb: (1−c) aabb,* or
> *c AaBb: (1−c) Aabb: (1−c) aaBb: c aabb.*

Bernstein takes

$$y = [AaBb + aabb] \ [Aabb + aaBb],$$

that is to say, the product of the sum of the numbers of $AaBb$ and $aabb$ offspring and of $Aabb$ and $aaBb$ offspring. He shows that its mean value

$$\bar{y} = s \ (s-1)x$$

and its standard deviation is given by

$$\sigma y^2 = s(s-1)x\left[(s-1) + (6 - {}^4\!s)x\right]$$

Hence from n such families the value of x is

$$\frac{1}{s^2 - s}\Sigma y$$

and its squared standard deviation is given by

$$\frac{x[s - 1 + (6 - 4s)x]}{n(s^2 - s)}$$

Wiener takes

$$V = [AaBb + aabb] \quad or \quad [Aabb + aaBb],$$

whichever is smaller, and finds

$$Q = \frac{1}{s}\Sigma V.$$

He then shows that

$$Q = x + x^2 + 2x^3 + 5x^4 + 14x^5 + \ldots$$

the number of terms being $\frac{1}{2}s$ if s is even, or $\frac{1}{2}(s - 1)$ if s is odd. The above series is the expansion of c in terms of x, *i.e.*,

$$\frac{1}{2}[1 - (1 - 4x)^{1/2}].$$

Also

$$\sigma Q^2 = \frac{1}{n}\left[Q - Q^2 - \frac{(s-1)x}{s}\right],$$

whence

$$\sigma x^2 = \frac{Q - Q^2 - \frac{(s-1)x}{s}}{n\left(\frac{dQ}{dx}\right)}$$

and

$$\frac{dQ}{dx} = 1 + 2x + 6x^2 + 20x^3 + 70x^4 + \ldots,$$

the appropriate number of terms being taken.

The efficiency of the two methods is the same when s becomes infinite, since in each case σx^2 tends to the value

$$\frac{x(1 - 4x)}{ns}.$$

When s is finite we compare the values of σx^2 when linkage is very slight, *i.e.*, $x = \frac{1}{4}$. This enables us to compare the efficiency of the methods when they are used for the detection of slight linkage. Bernstein's method now gives

$$\sigma x^2 = \frac{1}{8ns(s-1)},$$

Wiener's giving

$$\sigma x^2 = \frac{Q_o - Q_o{}^2 - \dfrac{s-1}{4s}}{n \left(\dfrac{dQ_o}{dx}\right)^2},$$

where Q_o and $\left(\dfrac{dQ_o}{dx}\right)$ are the values obtained on putting $x = \frac{1}{4}$ in the formulae for Q and $\dfrac{dQ}{dx}$. The relative efficiency of Wiener's method is the quotient of these two expressions and is given in Table I.

TABLE I

Size of family, s	2	3	4	5	6	7	8	9	10	11	∞
Relative efficiency of Wiener's method as percentage	100	100	85.7	94.7	85.1	93.1	85.0	91.2	85.3	91.4	100

Thus for families containing more than three members, Wiener's method is less efficient than Bernstein's, but the efficiency does not fall below 85 per cent. It may be added that Bernstein's method can be improved in certain other cases, as Wiener has pointed out. A paper on this topic is in preparation.

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